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Keys to subfamilies, tribes, genera and subgenera of the Gerridae of the World*

BY

HERBERT B. HUNGERFORD and RYUICHI MATSUDA

ABSTRACT: This paper presents keys for the identification of subgenera, genera, and higher categories of the five subfamilies of the waterstrider family Gerridae. The groupings are as follows: Rhagadotarsinae with two genera and four subgenera; Trepobatinae with thirteen genera; Halobatinae including the tribe Halobatini with two genera, and the tribe Metrocorini with seven genera and two subgenera; Ptilomerinae with eight genera and two subgenera; Gerrinae including the tribe Cylindrostethini with three genera, the tribe Charmatometrini with three genera, the tribe Gerrini with ten genera and eight subgenera, and the tribe Eotrechini with four genera.

When we began this and the following detailed study by the junior author we had available in the Francis Huntington Snow Entomological collections of the University of Kansas eighty-nine percent of the known genera and subgenera of the Gerridae of the world. The collections also contained the types of many species described by Hungerford and his students (Anderson, Shaw, Kenaga, Kuitert), by Drake and Harris, by Kirkaldy and by Torre-Bueno. There were paratypes of species described by Drake and Harris, Esaki, China, Drake, Hussey, Usinger, Hoberlandt and a number of others. We also had specimens determined by Kiritschenko and Poisson which were most helpful.

Of the genera not represented in our collection we have been able to borrow for study representative species of seven genera through the kindness of Dr. W. E. China and Dr. E. S. Brown of the British Museum, Dr. T. Jaczewski of the Polish Academy of Sciences, Dr. P. Basilevsky of the Royal Museum of Belgian Congo, Dr. A. Collart of the Royal Institute of Natural Sciences of Belgium, Drs. A. Soos and E. Halasfy of the Hungarian National Museum, Dr. R. Poisson of the University of Rennes, France, Dr. S. Miyamoto of the Kyushu University, Japan, and Miss L. C. Chen of the National Taiwan University, to all of whom we are most grateful. Of the three genera we have not seen, the type of one has never been located at any museum (*Rheumatotrechus himalayanus* Kirkaldy).

During our studies of the Gerridae we have published many papers

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describing new genera, subgenera and species, raising subgenera to genera, reducing genera to subgenera or synonymizing genera so that the information could be used in reporting the present study. As we bring them to a close we recognize fifty-three genera and sixteen subgenera in the Gerridae and the possibility of at least another subgenus, a question we cannot settle without more material.

The keys which are given below are followed by six plates illustrating all but three of the recognized genera. There are sixty-four of these wash-drawings. The figures referred to beyond these sixty-four are to be found in the succeeding paper by the junior author (Morphology, Evolution and a Classification of the Gerridae); certain page numbers also refer to the latter work. These structural drawings are useful in understanding the keys and must be studied before undertaking to use the keys.

KEY TO SUBFAMILIES

1\. Metacetabular suture in wingless forms dorsally continues to posterior margin of mesonotum, forming secondary definitive intersegmental suture between mesonotum and metanotum.* Without anteriorly produced primary intersegmental suture laterally in front of metathoracic spiracle (figs. 78-81, 107) 2

1\. Metacetabular suture in wingless forms dorsally not continuous to posterior margin of mesonotum, not forming secondary definitive intersegmental suture between mesonotum and metanotum (exception Cylindrostethini *). Primary intersegmental suture anteriorly produced laterally in front of metathoracic spiracle, or the suture lost laterally or rarely dorsolaterally lost (figs. 72-77, 107) 3

2\. First abdominal ventrite present (fig. 96) *Rhagadotarsinae* Lundblad, p. 319

2\. First abdominal ventrite absent (fig. 94) .. *Trepobatinae* Matsuda, p. 330

3\. Metacetabular suture dorsally reaching anterior end of first abdominal tergite and intersegmental suture between mesonotum and metanotum always distinct laterally. Metacetabular region thus always appears to be divided into two areas (figs. 72, 73) .... *Ptilomerinae* Bianchi, p. 260

3\. Metacetabular suture not reaching anterior end of first abdominal tergite (except for a few genera of Halobatinae). Intersegmental suture either lost laterally or rarely retained laterally. Metacetabular region thus never divided into two areas (figs. 74-77) 4

4\. Metasternum clearly present, at least about one tenth as long as mesosternum in length .... *Gerrinae* Amyot and Serville, p. 160

4\. Metasternum represented by a very short transverse, subtriangular plate rarely reaching metacetabular region laterally, or rarely by omphalium only .... *Halobatinae* Bianchi, p. 289

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* In Cylindrostethini the metacetabular region is divided into two areas but the metacetabular suture dorsally reaches the intersegmental suture (posterior margin of mesonotum), not the anterior end of the first abdominal tergite. In the genera of Halobatinae, in which the metacetabular suture reaches the anterior end of the first abdominal tergite, the intersegmental suture is lost laterally, thus the metacetabular region is not divided into two areas.

KEY TO GENERA OF RHAGADOTARSINAE

1\. Distal tarsal segment of front leg cleft at tip, with claws arising from base of the cleft. Eighth abdominal segment of both sexes elongate and nearly cylindrical. Males with a longitudinal depression on venter of seventh and eighth segments (fig. 37) .... *Rhagadotarsus* Breddin 2, p. 322

1\. Distal tarsal segment of front leg not cleft at tip but claws arising preapically from beneath. Eighth abdominal segment of both sexes not elongate as described above (fig. 39) *Rheumatobates* Bergroth 3, p. 326

2\. Pronotum in wingless forms short, one quarter the length of head. Mesothorax slightly wider than long. Hind coxae visible from above (fig. 37) .... R. (*Rhagadotarsus*) Breddin, p. 326

2\. Pronotum longer, one half the length of head. Mesothorax plainly longer than wide. Hind coxae not visible from above (fig. 38) .... *R. (Caprivia)* China, p. 326

3\. Anterior femur of male may be stout but lacks tuft of stout hairs on anterior margin.......... *R. (Rheumatobates)* Bergroth, p. 329

3\. Anterior femur of male stout, with a tuft of stout hairs on anterior margin (fig. 941) .... *R. (Hynesia)* China, p. 329

KEY TO GENERA OF TREPOBATINAE

1\. Hind femur distinctly longer than length of body. Second and third antennal segments swollen at distal ends and often bearing conspicuous spine clump in male. Hind tarsus with elongate, knife blade shaped claws at or before middle of second tarsal segment (fig. 57) .... *Metrobates* Uhler, p. 362

1\. Hind femur as long as or shorter than length of body. Second and third antennal segments without apical modifications mentioned above. Hind tarsus with claws not as described above 2

2\. Intersegmental suture between mesonotum and metanotum carinated (fig. 54) .... *Hynesionella* Poisson, p. 359

2\. Intersegmental suture between mesonotum and metanotum not carinated 3

3\. First antennal segment considerably longer than second and third segments together (fig. 52) *Trepobatoides* Hungerford and Matsuda, p. 343

3\. First antennal segment at most as long as second and third segments together 4

4\. First middle tarsal segment over twice as long as second middle tarsal segment 5

4\. First middle tarsal segment distinctly less than twice as long as second middle tarsal segment 6

5\. Head between eyes greatly widened posteriorly in female. Eyes overlapping less than half of propleuron. Male front tibia strongly arched. (figs. 62, 63) ...... *Rheumatometra* Kirkaldy, p. 364

5\. Head between eyes subquadrangular, very slightly widened posteriorly in female. Eyes overlapping most of propleuron. Male front femur and tibia not arched (fig. 53) *Metrobatopsis* Esaki, p. 367

6. Third antennal segment over twice as long as second segment, and distinctly longer than first segment 7
6. Third antennal segment less than one and a half times as long as second, distinctly shorter than first 8
7. First antennal segment nearly straight, not reaching beyond eyes. Anterior margins of first and second abdominal tergites completely absent. Metanotum without median longitudinal sulcus. South East Asia (fig. 51) .... *Cryptobates* Esaki, p. 355
7. First antennal segment distinctly curved near base and reaching behind eyes. Anterior margin of first and second tergites recognizable laterally. Median longitudinal sulcus of metanotum normally absent (fig. 59) .... *Telmatometra* Bergroth, p. 340
8. Omphalium distinctly present 9
8. Omphalium absent or occasionally vestigial 10
9. Omphalium very conspicuous, located on strongly anteriorly produced anterior margin of metasternum (fig. 58) *Stenobates* Esaki, p. 353
9. Omphalium not conspicuous, anterior margin of metasternum not strongly produced anteriorly (fig. 56) *Rheumatometroides* Hungerford and Matsuda, p. 351
10. Mesopleura without distinct longitudinal stripe (see fig. 61) *Naboandelus* Distant, p. 357
10. Mesopleura with distinct black, or yellow, or brown longitudinal stripe 11
11. Middle tibia distinctly shorter than length of body (fig. 55) *Ovatametra* Kenaga, p. 348
11. Middle tibia about as long as or a little longer than length of body 12
12. Eyes not extending beyond middle of propleura in side view. Hind tibia distinctly less than twice as long as tarsus (fig. 60) *Trepobates* Uhler, p. 337
12. Eyes extending beyond anterior half of propleura. Hind tibia over twice as long as tarsus (fig. 50) .... *Halobatopsis* Bianchi, p. 346

KEY TO TRIBES, GENERA AND SUBGENERA OF HALOBATINAE

1. Clypeus with basal margin well defined, anterior margin of head not smoothly rounded. Marine in habitat *Halobatini* Bianchi 2, p. 294
1. Clypeus with basal margin obliterated or lost. Anterior margin of head broadly and smoothly rounded. Fresh water in habitat .... *Metrocorini* Matsuda 3, p. 301
2. Long hairs confined to middle tibia (fig. 40) .. *Asclepios* Distant, p. 297
2. Long hairs present on tibia and first tarsal segment of middle leg (fig. 41) .... *Halobates* Eschscholtz, p. 299
3. Metanotum with lateral longitudinal elevation * reaching intersegmental suture between mesonotum and metanotum. Male third antennal segment has stiff hairs on margins (fig. 44) *Esakia* Lundblad, p. 316

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* Appears to be forward continuation of the abdominal connexivum.

3. Metanotum with lateral longitudinal elevation not reaching intersegmental suture between mesonotum and metanotum. Male third antennal segment without stiff marginal hairs 4
4. Eyes overlapping anterolateral angles of mesonotum 5
4. Eyes not overlapping anterolateral angles of mesonotum 6
5. Posterolateral angles of metacetabula simple. Male without a tubercle either on mesosternum or on inner margin of front femur .... *Ventidius (Ventidius)* Distant, p. 313
5. Posterolateral angles of metacetabula bilobed. Male with a tubercle on mesosternum and on inner margin of front femur (fig. 43) ..... *Ventidius (Ventidioides)* Hungerford and Matsuda, p. 315
6. Metasternum represented practically by a small omphalial pore (fig. 48) .... *Eurymetropsiella* Poisson, p. 307
6. Metasternum represented either by a transverse subtriangular lobe, or posteriorly produced conical plate bearing omphalium, 7
7. Metasternum represented by a conical plate produced posteriorly (fig. 49) .... *Eurymetropsielloides* Poisson, p. 309
7. Metasternum represented by a transverse subtriangular plate, its anterior margin more or less strongly produced anteriorly .. 8
8. Mesonotal region with a median longitudinal and lateral paired oblique black stripes 9
8. Mesonotal region predominantly black, without black longitudinal stripes. Male pygophore bifurcates apically (fig. 46)
Eurymetropsis Poisson, p. 311
9. Body flattened and often lustrous above. Female seventh abdominal segment with ventral apical margin simply concave (fig. 47) .... *Eurymetra* Esaki, p. 305
9. Body flattened and dull in color above. Female seventh abdominal segment with ventral apical margin excessively developed and modified in various shapes, hiding eighth segment (fig. 45) .... *Metrocoris* Mayr, p. 302

KEY TO GENERA AND SUBGENERA OF PTILOMERINAE

1. Hind tarsal segments fused 2
1. Hind tarsal segments distinct from each other 4
2. Lateral longitudinal suture of mesonotum distinct. Female abdomen withdrawn into thoracic cavity (fig. 28)
Potamometra Bianchi, p. 271
2. Lateral longitudinal suture of mesonotum absent. Female abdomen is not withdrawn into thoracic cavity 3
3. Hind coxa without a spine. Seventh segment of female without lateral lobes (fig. 33)
Ptilomera (Proptilomera) Hungerford and Matsuda, p. 270
3. Hind coxa with a spine. Seventh segment of female with conspicuous lateral lobes (fig. 36)
Ptilomera (Ptilomera) Amyot and Serville, p. 270
4. Anterior margin of head rounded. First antennal segment shorter than three following segments together (fig. 32)
Rheumatogonus Kirkaldy, p. 283

4. Anterior margin of head not rounded. First antennal segment about as long as or longer than three following segments together 5
5. First hind tarsal segment shorter than second. Female seventh abdominal segment without narrow, long and spinous process. Metanotum in female without median elevated process on hind margin 6
5. First hind tarsal segment twice as long as second. Female seventh abdominal segment with narrow, long and spinous process. Metanotum in female with median elevated process on hind margin .... *Pleciobates* Esaki, p. 286
6. Middle and hind tarsi with distinct claws (fig. 30) *Potamometropsis* Lundblad, p. 281
6. Middle and hind tarsi without distinct claws 7
7. Hind coxa long and cylindrical, twice as long as basal width. Female abdomen telescoped into thoracic cavity and its metacetabula with a fingerlike process on inner rear margin (figs. 34, 35) .... *Potamometroides* Hungerford, p. 278
7. Hind coxa shorter, not cylindrical, basally broader. Female abdomen not telescoped into thoracic cavity, its metacetabula without a projecting process 8
8. Front femur without or with one or two indefinite dorsolateral bands. Caudal margin of pronotum straight or concave. Mesothorax with sides converging cephalad and anterolateral angles sloping, not prominent. Female venter normal (fig. 29) .... *Rhyacobates* Esaki, p. 273
8. Front femur with two dorsolateral longitudinal black bands. Caudal margin of pronotum faintly undulate, its median lobe slightly produced caudally. Mesothorax with sides nearly parallel and anterolateral angles prominent and transverse. Female venter with well-demarcated flattened area (fig. 31) *Heterobates* Bianchi, p. 276

KEY TO TRIBES OF GERRINAE

1. Metacetabular suture connected dorsally with dorsal posterior margin of mesonotum (intersegmental suture) *Cylindrostethini* Matsuda, p. 217
1. Metacetabular suture not connected with intersegmental suture dorsally 2
2. Anterior margin of first abdominal tergite straight *Charmatometrini* Matsuda, p. 233
2. Anterior margin of first abdominal tergite bisinuate (flattened W-shaped) 3
3*. Pronotum prolonged primitively. Connexival spine present primitively. Apical segment of endosoma always provided with ventral plate .... *Gerrini* Amyot and Serville, p. 163

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* These two characters indicate fundamental differences in evolutionary trends. For separation of the genera of Gerrini and Eotrechini, see the key to genera of Gerrinae.

3*. Pronotum not prolonged. Connexival spine absent primitively. Apical segment of endosoma with very poorly developed ventral plate or without it, and apical plate greatly developed . . . . *Eotrechini* Matsuda, p. 243

KEY TO GENERA OF GERRINAE †

1. Hind leg longer than middle leg 2
1. Hind leg nearly as long as or shorter than middle leg 3
2. Metasternum with omphalial groove present. Claws arising preapically. Gigantic in size (fig. 3)
Gigantometra Hungerford and Matsuda, p. 171
2. Metasternum without omphalial groove. Claws arising apically. Moderate in size (fig. 25) . . . . *Eotrechus* Kirkaldy, p. 249
3. Metacetabular suture reaching dorsally to intersegmental suture between mesonotum and metanotum 4
3. Metacetabular suture not reaching dorsally to intersegmental suture between mesonotum and metanotum 6
4. Body strongly flattened and short, without omphalial groove (fig. 20) . . . . *Platygerris* B. White, p. 231
4. Body not flattened, cylindrical or at least not short. With omphalial groove 5
5. Abdominal spiracles located closer to anterior margins than to posterior margins of segments.** Male pygophore not rotated. Body more or less cylindrical (figs. 17, 18)
Cylindrostethus Fieber, p. 224
5. Abdominal spiracles located at middles of segments.* Male pygophore rotated. Body shorter (fig. 19)
Potamobates Champion, p. 228
6. Omphalial groove present 7
6. Omphalial groove absent 10
7. Pronotum relatively short. Mesosternum about twice as long as metasternum (fig. 9) . . *Gerriselloides* Hungerford and Matsuda, p. 187
7. Pronotum long. Mesosternum at least five times as long as metasternum 8
8. Middle femur longer than middle tibia 9
8. Middle femur shorter than middle tibia (fig. 23)
Brachymetra Mayr, p. 240
9. Pronotum with four black longitudinal stripes, marginal ones confluent posteriorly. First tarsal segment of front leg shorter than second (fig. 22) . . . . *Eobates* Drake and Harris, p. 242
9. Pronotum without black longitudinal stripes, concolorous brown. First tarsal segment of front leg longer than second (fig. 21) . . . . *Charmatometra* Kirkaldy, p. 238
10. First tarsal segment of middle and hind legs shorter than second. Claws arising from near middle of second segment and conspicuous (fig. 26) . . . . *Onychotrechus* Kirkaldy, p. 251

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† *Rheumatotrechus* Kirkaldy is not included.

** In *Potamobates thomasi* Hungerford the spiracle is placed closer to the anterior margin than to the posterior margin of each segment.

10. First tarsal segment of middle and hind legs longer than second. Claws inconspicuous and arising from near apex of second segment 11

11. Mesonotum with paired oblique depressions near anterior margin. Paramere greatly developed (fig. 27)
Chimarrhometra Distant, p. 254

11. Mesonotum without paired oblique depression near anterior margin 12

12. Hind coxa distinctly longer than wide. Pronotum not prolonged (fig. 24) . . . . *Amemboa* Esaki, p. 256

12. Hind coxa shorter than wide or as wide as long. Pronotum prolonged in most species 13

13. Hind tibia less than one fourth as long as hind femur. Male suranal plate with conspicuous spinous process on each side (figs. 10, 11) . . . . *Gerrisella* Poisson, p. 189

13. Hind tibia over one-third as long as hind femur. Male suranal plate without conspicuous spinous process 14

14. Pronotum with a median black longitudinal stripe 15

14. Pronotum with a median yellow longitudinal stripe 18

15. Pronotum not prolonged (fig. 16)
Tenagogonus (Tenagometra) Poisson, p. 213

15. Pronotum prolonged 16

16. Rostrum with third segment not reaching onto mesosternum (fig. 12) . . . . *Tenagogerris* Hungerford and Matsuda, p. 191

16. Rostrum with third segment reaching onto mesosternum 17

17. Male abdomen short, 7th, 8th and 9th segments together at least as long as four preceding segments. Male without connexival segment produced into triangular flattened plate or nexival spine . . . . *Tenagogonus (Tenagogonus)* Stål, p. 209

17. Male abdomen not reduced, 7th, 8th and 9th segments together shorter than four preceding segments. Male 7th connexival segment produced into triangular flattened plate or spinelike process (fig. 4) . . . . *Tenagogonus (Limnometra)* Mayr, p. 209

18. Mesopleuron with two large white spots. Legs and antennae in male about three times longer than in female (fig. 1)
Tenagometrella Poisson, p. 214

18. Mesopleuron without two large white spots. Legs and antennae nearly equal in length in both sexes 19

19. Second antennal segment as long as or longer than third, or a little shorter than third 20

19. Second antennal segment much shorter than third (fig. 2)
Tachygerris Drake, p. 202

20. Pronotum shiny in most species. Pronotum either with a median longitudinal yellow stripe and lateral short yellow stripes, or the lateral stripes alone, or with a large yellow spot alone on anterior lobe 21

20. Pronotum dull, always with a median yellow longitudinal stripe which is obliterated on posterior lobe and often with a pair of large black spots on either side of median yellow longitudinal stripe 22

21. Pronotum with median yellow longitudinal stripe reaching posterior margin of pronotum and always with a pair of short concolorous lateral stripes one on either side of median longitudinal stripe (fig. 7) .... *Limnogonus (Limnogonus)* Stål, p. 200
21. Pronotum with a large median yellow spot on anterior lobe (fig. 8) .. *Limnogonus (Limnogonellus)* Hungerford and Matsuda, p. 200
22. First antennal segment considerably shorter than second and third segments together 23
22. First antennal segment longer than or equal to or slightly shorter than second and third segments together 24
23. Relatively broad and short species. Hind femur about as long as middle femur. Metathoracic spiracle placed more than its own length from pronotum. Pronotum not fully prolonged (fig. 5) .... *Eurygerris* Hungerford and Matsuda,* p. 194
23. More slender and more elongate species. Hind femur distinctly longer than middle femur. Metathoracic spiracle placed less than its own length from pronotum. Pronotum fully prolonged (fig. 14) .... *Gerris (Limnoporus)* Stål, p. 184
24. Hind tibia about three times (never over 3.2 times) as long as first tarsal segment. First antennal segment about equal to or a little shorter than two following segments together * (fig. 13) *Gerris (Gerris)* Fabricius, p. 179
24. Hind tibia at least four times as long as hind first tarsal segment. First antennal segment about equal to or a little longer than two following segments together ** (fig. 15) *Gerris (Aquarius)* Schellenberg, p. 175

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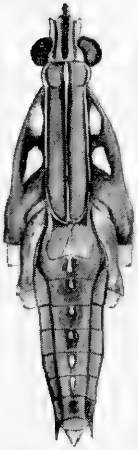
* In *E. mexicanus* (Champion) the posterior lobe of pronotum is almost fully prolonged.

** The antennal character is not satisfactory for determining New World *Aquarius*.

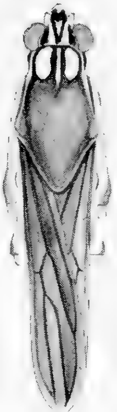
FIGURES 1-12

1. *Tenagometrella longicornis* (Poisson), female.
   Length of body: 12.4 mm.
2. *Tachygerris quadrilineatus* (Champion), male.
   Length of body: 6.85 mm.
3. *Gigantometra gigas* (China), male.
   Length of body: 31.9 mm.
4. *Tenagogonus (Limnometra) femoratus* (Mayr) male.
   Length of body: 18.0 mm.
5. *Eurygerris fuscinervis* (Berg), male.
   Length of body: 6.4 mm.
6. *Tenagogonus (Tenagogonus) albovittatus* Stål, male.
   Length of body: 6.55 mm.
7. *Limnogonus (Limnogonus) hyalinus* (Fabricius), male.
   Length of body: 8.53 mm.
8. *Limnogonus (Limnogonellus) hesione* (Kirkaldy), female.
   Length of body: 6.15 mm.
9. *Gerriselloides brachynotus* (Horvath), female.
   Length of body: 7.6 mm.
10. *Gerrisella settembrinoi* (Poisson), winged male.
   Length of body: 5.2 mm.
11. *Gerrisella settembrinoi* (Poisson), wingless male.
   Length of body: 4.5 mm.
12. *Tenagogerris euphrosyne* (Kirkaldy), wingless female.
   Length of body: 6.4 mm.

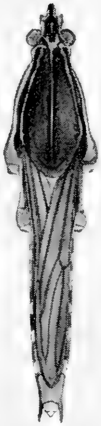
FIGURES 1-12



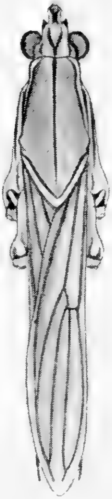
1 Tenagometrella longicornis



2 Tachygerris quadrilineatus

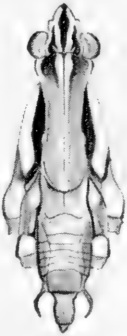


3 Gigantometra gigas

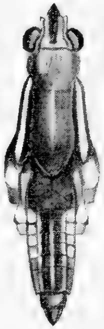


4 Tenagogonus (Limnometra) femoratus

5 Eurygerris fuscinervis

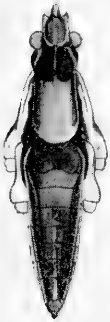


6 Tenagogonus (Tenagogonus) albovittatus



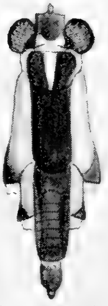
7 Limnogonus (Limnogonus) hyalinus

8 Limnogonus (Limnogonellus) hesione

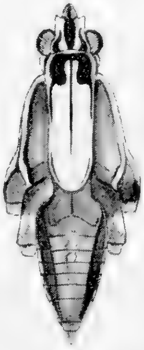


9 Gerriselloides brachynotus

10 Gerrisella settembrinoi



11 Gerrisella settembrinoi

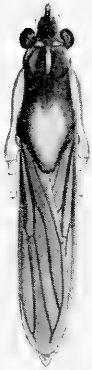


12 Tenagogerris euphrosyne

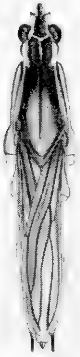
FIGURES 13-24

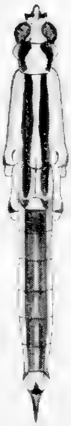
13. *Gerris (Gerris) thoracicus* Schummel, winged female.
    Length of body: 11.4 mm.
14. *Gerris (Limnoporus) rufoscutellatus* (Latreille), winged male.
    Length of body: 13.6 mm.
15. *Gerris (Aquarius) paludum* Fabricius, winged male.
    Length of body: 15.1 mm.
16. *Tenagogonus (Tenagometra)* sp., wingless female.
    Length of body: 6.1 mm.
17. *Cylinorostethus palmaris* Drake and Harris, wingless male.
    Length of body: 16.2 mm.
18. *Cylindrostethus productus* Spinola, winged female.
    Length of body: 27.0 mm.
19. *Potamobates unidentatus* Champion, wingless male.
    Length of body: 8.7 mm.
20. *Platygerris depressus* B.-White, wingless male.
    Length of body: 5.8 mm.
21. *Charmatometra bakeri* Kirkaldy, wingless female.
    Length of body: 13.5 mm.
22. *Eobates vittatus* (Shaw), wingless male.
    Length of body: 7.5 mm.
23. *Brachymetra kleopatra* Kirkaldy, wingless male.
    Length of body: 8.0 mm.
24. *Amemboa fumi* Esaki, wingless female.
    Length of body: 4.1 mm.

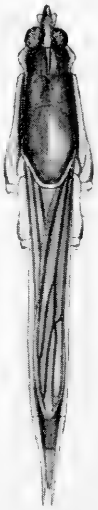
FIGURES 13-24

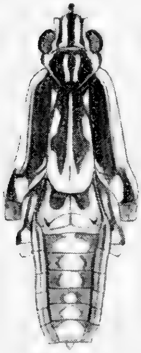

13 Gerris (Gerris) thoracicus

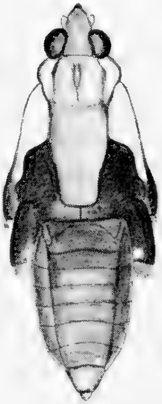

14 Gerris (Limnoporus) rufoscutellatus

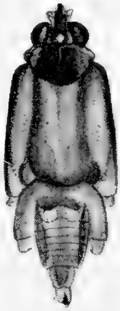

15 Gerris (Aquarius) paludum

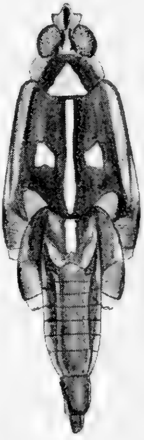

17 Cylindrostethus palmaris

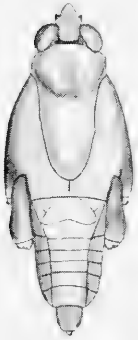

18 Cylindrostethus productus

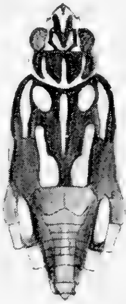

16 Tenagogonus (Tenagometra) sp.

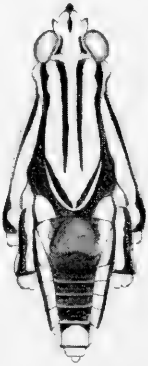

21 Charmatometra bakeri


20 Platygerris depressus


19 Potamobates unidentatus


23 Brachymetra kleopatra


24 Amemboa fumi

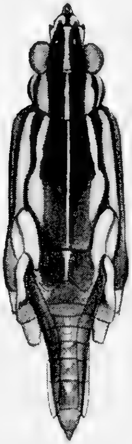

22 Eobates vittatus

FIGURES 25-35

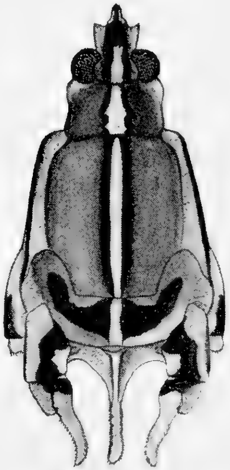
25. *Eotrechus kalidasa* Kirkaldy, winged male.
    Length of body: 10.2 mm.
26. *Onychotrechus sakuntala,* Kirkaldy, wingless female.
    Length of body: 6.5 mm.
27. *Chimarrhometra orientalis* (Distant), wingless male.
    Length of body: 7.2 mm.
28. *Potamometra berezowskii* Bianchi, wingless female.
    Length of body: 16.2 mm.
29. *Rhyacobates takahashii* Esaki, wingless female.
    Length of body: 9.2 mm.
30. *Potamometropsis werneri* Hungerford, wingless female.
    Length of body: 8.2 mm.
31. *Heterobates dohrandti* Bianchi, wingless male.
    Length of body: 7.1 mm.
32. *Rheumatogonus burmanus,* Distant, wingless female.
    Length of body: 6.8 mm.
33. *Ptilomera* (*Proptilomera*) *himalayensis* Hungerford and Matsuda, winged male.
    Length of body: 10.4 mm.
34. *Potamometroides madagascariensis* Hungerford, wingless male.
    Length of body: 6.5 mm.
35. *Potamometroides madagascariensis* Hungerford, wingless female.
    Length of body: 5.8 mm. (as for coxa)

FIGURES 25-35

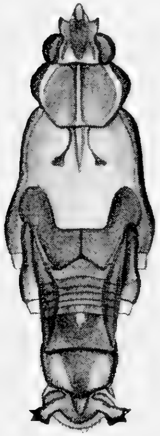
25 Eotrechus kalidasa



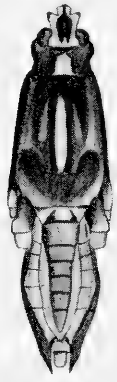
26 Onychotrechus sakuntala



28 Potamometra berezowskii

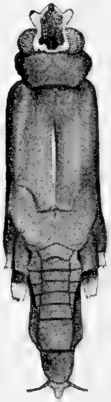


27 Chimarrhometra orientalis

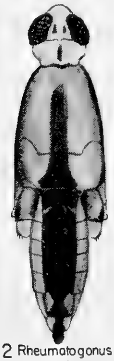


29 Rhyacobates takahashii

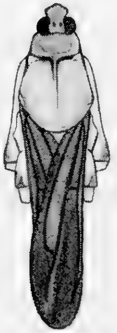
30 Potamometropsis werneri



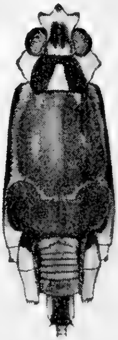
31 Heterobates dohrandti



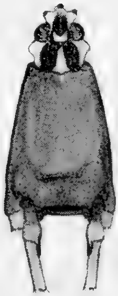
32 Rheumatogonus burmanus



33 Ptilomera (Proptilomera) himalayensis



34 Potamometroides madagascariensis

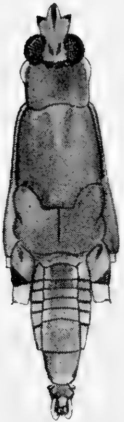


35 Potamometroides madagascariensis

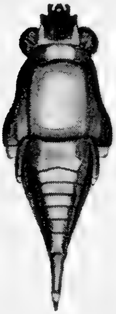
FIGURES 36-45

36. *Ptilomera* (*Ptilomera*) *werneri* Hungerford and Matsuda, winged male.
Length of body: 11.0 mm.
37. *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin, wingless male.
Length of body: 3.1 mm.
38. *Rhagadotarsus (Caprivia)* hutchinsoni China, wingless female.
Length of body: 5.4 mm.
39. *Rheumatobates rileyi* Bergroth, wingless female.
Length of body: 2.6 mm.
40. *Aschepios apicalis* Esaki, wingless male.
Length of body: 2.6 mm.
41. *Halobates sobrinus* B.-White, wingless male.
Length of body: 4.0 mm.
42. *Ventidius (Ventidius) malayensis* Hungerford and Matsuda, wingless male.
Length of body: 3.9 mm.
43. *Ventidius (Ventidioidis) kuiterti* Hungerford and Matsuda, wingless male.
Length of body: 2.4 mm.
44. *Esakia kuiterti* Hungerford and Matsuda, wingless female.
Length of body: 2.2 mm.
45. *Metrocoris strangulator* Breddin, wingless male.
Length of body: 5.05 mm.

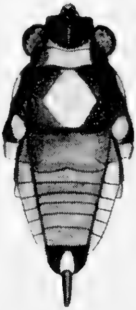
FIGURES 36-45



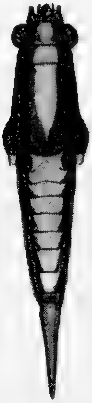
36 ptilomera(Ptilomera) werneri



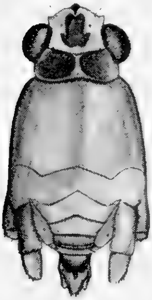
37 Rhagadotarsus (Rhagadotarsus) kraepelini



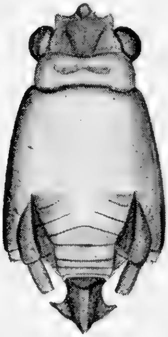
39 Rheumatobates rileyi



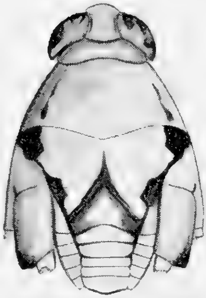
38 Rhagadotarsus (Caprivia) hutchinsoni



40 Asclepios apicalis

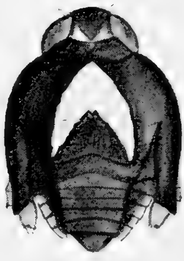


41 Halobates sobrinus

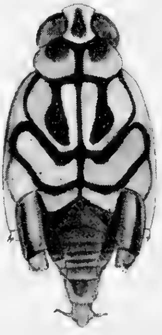


42 Ventidius (Ventidius) malayensis

43 Ventidius (Ventidioides) kuiterti



44 Esakia kuiterti



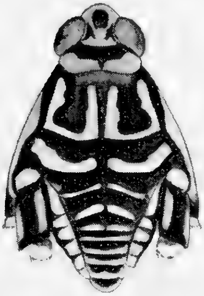
45 Metrocoris strangulator

FIGURES 46-54

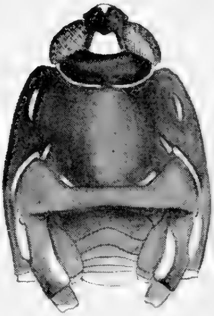
46. *Eurymetropsis carayoni* Poisson, wingless male.
    Length of body: 5.2 mm.
47. *Eurymetra natalensis* (Distant), wingless female.
    Length of body: 4.9 mm.
48. *Eurymetropsiella schoutedeni* Poisson, wingless female.
    Length of body: 3.8 mm.
49. *Eurymetropsielloides milloti* Poisson, wingless male.
    Length of body: 3.5 mm.
50. *Halobatopsis platensis* (Berg), wingless male.
    Length of body: 3.5 mm.
51. *Cryptobates raja* (Distant), wingless male, genital segments removed.
    Length of body: 3.2 mm.
52. *Trepobatoides boliviensis* Hungerford and Matsuda.
    Length of body: 3.8 mm.
53. *Metrobatopsis flavonotatus* Esaki, wingless female.
    Length of body: 2.4 mm.
54. *Hynesionella omercooperi* Hungerford and Matsuda.
    Length of body: 2.35 mm.

FIGURES 46-54

46 Eurymetropsis carayoni

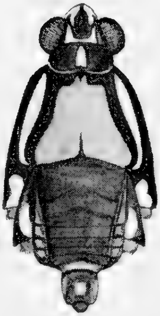


47 Eurymetra natalensis

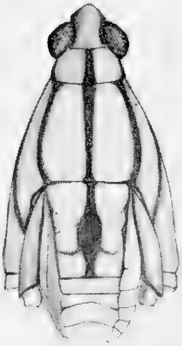


48 Eurymetropsiella schoutedeni

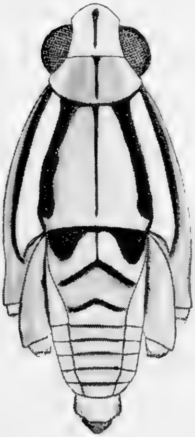
49 Eurymetropsielloides milloti



50 Halobatopsis platensis

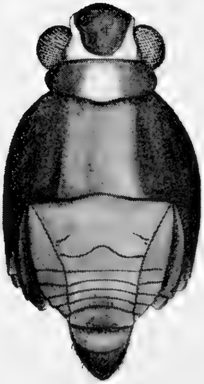


51 Cryptobates raja



52 Trepobatoides boliviensis

53 Metrobatopsis flavonotatus

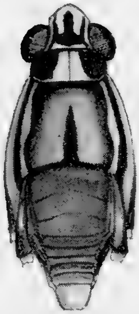


54 Hynesionella omercooperi

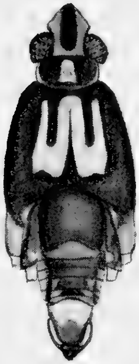
FIGURES 55-64

55. *Ovatametra minima* Kenaga, wingless male.
Length of body: 2.1 mm.
56. *Rheumatometroides browni* Hungerford and Matsuda.
Length of body: 3.2 mm.
57. *Metrobates hesperius* Uhler, wingless male.
Length of body: 4.1 mm.
58. *Stenobates biroi* (Esaki), wingless male.
Length of body: 4.05 mm.
59. *Telmatometra whitei* Bergroth, wingless female.
Length of body: 4.2 mm.
60. *Trepobates pictus* (Herrich-Schaeffer), wingless male.
Length of body: 3.3 mm.
61. *Naboandelus bergevini* Bergroth, wingless female.
Length of body: 2.55 mm.
62. *Rheumatometra philarete* Kirkaldy, wingless female.
Length of body: 3.15 mm.
63. *Rheumatometra philarete* Kirkaldy, wingless male.
Length of body: 2.3 mm.
64. *Hermatobates weddi* China, wingless male.
Length of body: 3.6 mm.

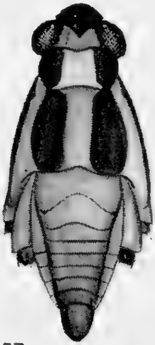
FIGURES 55-64



55 Ovatametra minima

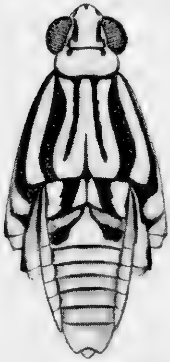


56 Rheumatometroides browni

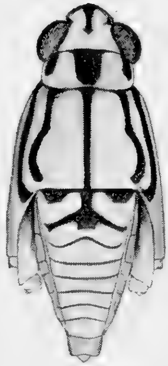


57 Metrobates hesperius

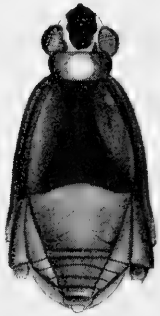
58 Stenobates biroi



59 Telmatometra whitei

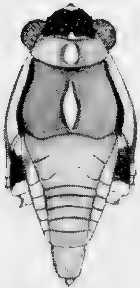


60 Trepobates pictus



61 Naboandelus bergevini

62 Rheumatomefra philarete



63 Rheumatometra philarete

64 Hermatobates weddi

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Morphology, Evolution and a Classification of the Gerridae (Hemiptera-Heteroptera) *

BY

RYUICHI MATSUDA
The University of Kansas

ABSTRACT: This work is a study of the morphology, evolution and classification of the Gerridae of the World. Fifty genera and sixteen subgenera out of fifty-three genera and sixteen subgenera known were examined.

In the section on morphology it is attempted to establish homologies and a terminology for as many external structures as possible. In the section on the structural evolution the process of evolutionary change of each structure is traced, and its taxonomic significance is discussed. The postembryonic development of the antennal and leg segments has been studied in representative species of each major group to see how the different proportional lengths of antennal and leg segments are realized ontogenetically; how the ontogenetic growth patterns for these segments have been carried over to adult phylogeny; and how the growth patterns themselves have evolved. It was found that (1) the antennal and leg segments show roughly a simple allometric growth, with either an appreciable increase or decrease in growth ratio at the final stage of development; (2) often lengths of the leg and antennal segments of adults in a great majority of species within a genus fall roughly on the growth lines for the corresponding segments in a representative species of the same genus, indicating that species within a genus share very similar growth patterns for corresponding segments; (3) a hypothetically primitive growth ratio for the antennal segments ($k = 1.142$) is suggested; (4) a process of development of the proximo-distal gradient in growth ratios for the antennal segments in the phylogeny of the Gerridae is traced; (5) for certain segments, such as the hind tibia, there is evidence in many genera that the growth patterns vary among species of a genus, thus forming the secondary phylogenetic allomorphic lines; (6) as a result of the formation of the secondary allomorphic slope for the hind tibia, which is always steeper than that for the hind femur, the tibia is shorter in relation to the femur in the smaller species of a given genus, and this tendency occurs in most major groups of the Gerridae; (7) since there is a striking tendency toward smaller body size in the structurally more specialized forms at all taxonomic levels, and the congeneric species often appear to have

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* The contribution number 1048 from the Department of Entomology, The University of Kansas. This study was made possible with the aid of a grant from the National Science Foundation.

very similar allometric growth patterns for corresponding antennal and leg segments, the lengths of antennal and leg segments in the early postembryonic developmental stages in larger and primitive species roughly approximate the lengths of the same in adults of related but phylogenetically more advanced forms. In the light of the knowledge gained from the study of evolution of the leg and antennal segments, the taxonomic status of all groups of the Gerridae (subfamilies, tribes, genera and subgenera) is evaluated.

The arrangement of genera in the proposed new classification of the Gerridae follows. Trepobatinae is described as a new subfamily and Hermatobatinae is excluded from the Gerridae.

(1) Gerrinae.

Gerrini, including *Gerris (Gerris s. str., Aquarius, Limnoporus), Gerriselloides, Gerrisella, Gigantometra, Tenagogerris, Eurygerris, Limnogonus (Limnogonus s. str., Limnogonellus), Tachygerris, Tenagogonus (Tenagogonus s. str., Limnometra, Tenagometra), Tenagometrella.*

Cylindrostethini, including *Cylindrostethus, Potamobates, Platygerris.*

Charmatometrini, including *Charmatometra, Brachymetra, Eobates.*

Eotrechini, including *Eotrechus, Onychotrechus, Chimarrhometra, Amemboa, Rheumatotrechus*(?).

(2) Ptilomerinae, including *Ptilomera (Ptilomera s. str., Proptilomera), Potamometra, Rhyacobates, Heterobates, Potamometroides, Potamometropsis, Rheumatogonus, Pleciobates.*

(3) Halobatinae.

Halobatini, including *Asclepios, Halobates.*

Metrocorini, including *Metrocoris, Eurymetra, Eurymetropsiella, Eurymetropsielloides, Eurymetropsis, Ventidius (Ventidius s. str., Ventidioides), Esakia.*

(4) Rhagadotarsinae, including *Rhagadotarsus (Rhagadotarsus s. str., Caprivia), Rheumatobates (Rheumatobates s. str., Hynesia).*

(5) Trepobatinae, including *Trepobates, Telmatometra, Trepobatoides, Halobatopsis, Ovatametra, Rheumatometroides, Stenobates, Cryptobates, Naboandelus, Hynesionella, Metrobates, Rheumatometra, Metrobatopsis.*

CONTENTS

INTRODUCTION

The objective of this work is to elucidate the structural evolution of the Gerridae of the World on a morphological basis, and to establish a new classification of the higher categories of this group of insects.

To attain these objectives the external morphology of some representative species of the Gerridae was studied with frequent comparison with other Hemiptera and other major groups of insects in order to establish homologies and a terminology of structures.

Having established the homologies and terminology of structures, the next step was to compare series of forms so as to trace the evolutionary changes of as many structures as possible. For certain structures, such as the antennae and legs, postembryonic development, in representative species of major groups, was studied to see how the different proportional lengths of the leg and antennal segments are realized ontogenetically, and how the ontogenetic growth patterns of these structures have been carried over to adult phylogeny, and how the growth patterns themselves have evolved.

In tracing the evolutionary changes of structures the following morphological principles were borne in mind: (1) that evolution has been continuous, each change being based upon stages that have gone before; (2) that evolutionary changes are to be accounted for by modification of pre-existed structures, by fusion of pre-existed structures, or by loss of pre-existed structures; (3) that evolution has not been merely endless change involving all structures of the body. There are structures which have remained relatively stable while others have changed. It is these stable structures which constitute the bases upon which we can depend for the tracing of continuity.

To decide which of the alternative characters is more primitive or specialized is a matter of probability in morphology, since paleontological data either to prove or disprove the morphological interpretations are often lacking or inadequate. This is especially true of the group of insects such as the Gerridae treated in this work. Therefore, the decisions that have been made in regard to which of two or more alternatives is more primitive or specialized can, by their very nature, not be final. The reliability of interpretations based on morphology, however, increases with increase of material with which to make comparison. Entomologists are in an almost ideal position in this respect, since the diversity of forms in insects is unparalleled in the animal kingdom, as stressed by the late Professor G. F. Ferris (1948).

In the third part of this work a new classification of higher categories of the Gerridae has been attempted with discussion of the phylogeny of the group thus defined. In discussing phylogeny of groups all significant characters were tabulated at the end of the description of each major group to show the over-all degree of primitiveness or specialization of each group or tribe, and to determine the number of characters each genus or tribe has in common with others. The characters selected, however, include those apparently resulting from parallelism. It was found that tabulation often prevents the errors that would result from more subjective judgments based on fewer, often prejudiced characters. The subfamilial, tribal and generic descriptions have been made quite full and include discussions of evolutionary changes of structures at the specific level, whenever enough species were available to allow observations on structural modifications. In describing subfamilies, tribes, and genera all characters are described in a parallel fashion in so far as possible. For three genera, however, no specimens were available for study, and in these cases the original descriptions have merely been repeated. Also any characters peculiar to a given group (genus, tribe, subfamily) are italicized, and these characters are excluded from the descriptions of the other groups.

In table 16, 82 units are equal to 10 mm. For those values with asterisks, 173.7 units are equal to 10 mm.; the figures under each leg correspond to the femur, tibia, and the first and second tarsal segments. The measurements of the third and fourth rostral segments were made as indicated by broken lines in figure 65. The relative lengths of leg and antennal segments given as characters 125, 126, 127, 128, 129 are based on the data for both sexes. In the tables of characters for major groups (+) indicates a primitive alternative; (—) a specialized; (±) an intermediate condition between the primitive and specialized alternatives, and (±)$^{\times}$ is the condition in which the primitive or specialized alternative is shared only by certain species or genera within a given group.

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EXTERNAL MORPHOLOGY

Gerris remigis Say was selected as the standard gerrid for the study of morphology of the external structures of the Gerridae because of its relative abundance, convenient size for dissection and relative primitiveness in structure. Other species were also studied to facilitate the interpretation of structures in this family. Unless otherwise stated the structures below are those of *Gerris remigis* Say.

The head

(Figs. 65-71)

The head is directed forward apically. The four segmented antennae are also directed anteriorly; the third and fourth segments are always pedunculated at bases in all species of Gerridae except for the fourth segment in Rhagadotarsinae. The rostrum is four segmented, is placed on the ventral surface of the head when at rest; the first segment is thick, about as long as wide; the second is shortest in all species of Gerridae; the third is longest also in all species of Gerridae, with a small apical lobe superposed on the dorsal basal region of the fourth segment; the lobe is clearly defined by the weak membranous region basally, which can be seen upon treatment with KOH. The fourth segment is always black in all species of Gerridae. The rostrum or beak is generally conceived to be labial in origin, the basal two segments corresponding to the postmentum and prementum and the apical two segments being represented by the paraglossa and the ligula in generalized insects.

The labrum is short, subtriangular, apically inserted into the dorsal basal region of the first rostral segment, basally well defined from the apical margin of the clypeus. The epipharynx arises from the clypeal region, is basally continuous with the food pump, apically inserted beneath the labrum into the second rostral segment. This prolonged epipharynx is said to be characteristic of Gerridae, Hydrometridae, and Veliidae (Servadei 1946).

The mandibular plate is externally separated from the maxillary plate by the transverse suture, which ventrally reaches inside the antennal cavity. The basal margin of the mandibular plate bears internally the elongate, subtriangular lever, which is in turn connected with the mandibular stylet; the mandibular stylet (seta) at its base is rectangularly curved behind the basal margin of the lever for the attachment of the muscle (fig. 70).

The maxillary plate lacks the maxillary lever; the maxillary stylet (fig. 71) is basally ensheathed by the setal pouch, which extends beyond the middle of mesothorax (foh. in the figures by Ekblom, 1926). This stylet is supported by the tendonous rod arising from the lateral angle of the foramen magnum. Ekblom (1926) regarded this rod as the tentorium (posterior tentorium). He recognized this enormously prolonged maxillary stylet and the rod (tentorium of Ekblom) in *Gerris asper* and *Velia currens*. A similar condition is also known in *Trepidotylus* of Plataspidae (Poisson 1951). The anterior tentorium is absent.

The salivary syringe is well sclerotized posteriorly, with a piston arising from the posterior end. The food pump is ventrally supported by a single, well-sclerotized, long plate. This is probably homologous to the hypopharyngeal wing in some groups of Heteroptera and Homoptera.

The clypeus is basally well defined. The eyes are indented and the ocelli are absent. The antenniferous tubercles are located far in front of the compound eyes. The two anterior pairs of trichobothria are located anterior to the eyes, and the basal pair is located near the basal angles of the compound eyes.

The thorax

The thorax of the Gerridae was studied by Taylor in *Gerris* sp. (1918), and by Larsén (1945) in *Gerris rufoscutellatus* Latreille. Matsuda (1957) studied the pterothoracic sutures of representative species of the Gerridae and discussed their taxonomic significance.

The prothorax

The pronotum is always prolonged in the winged forms, as well as in wingless forms of most groups of the Gerridae. The pronotum is divided into two areas, separated by an obscure transverse suture. The suture usually obsolete when the pronotum is more or less greatly prolonged, but distinctly marked when the pronotum is not greatly prolonged, as in *Eurygerris* (figs. 263, 264). The first phragma arises from beneath the suture. Thus the suture represents roughly the point where the prolongation starts, and it corresponds to the posterior margin of the pronotum in the wingless forms of the genera in which the pronotum is not prolonged. In the winged forms of all genera the pronotum is more or less widened and elevated above the point of the wing base. This point is called the humerus; in wingless forms the humerus is absent or only feebly developed when the vestigial wing pad occurs. It is common practice in the taxonomy of this group of insects to call the area anterior to the humeri the anterior lobe, and the area posterior to the humeri the posterior lobe in the winged forms, but this is inconvenient because the humerus is not produced in wingless forms. The transverse suture demarcating the point of origin of prolongation of the pronotum is more or less distinct, or at least traceable in both winged and wingless forms; therefore, the terms anterior and posterior lobes are applied to the regions anterior and posterior to the suture respectively in this work. The prosternum is indistinguishable from the propleural region and narrower than the meso- and metasternal regions. The prosternal apophysis is present but small.

The mesothorax and Wing bases

The mesothoracic spiracle is hidden beneath the pronotum, located lateral to the intersegmental membrane arising from beneath the transverse suture of the pronotum. In the mesonotum the antecostal suture demarcates the anterior margin except medially where the small lobate acrotergite extends forward. Paired parapsidial sutures run posteriorly from the anterior margin of the mesonotum. The area between these sutures was thought to be the prescutum by Taylor (1918) and Larsén (1945), but the prescutum by definition (Snodgrass 1935) is the area of the mesonotum or metanotum between the antecostal suture and prescutal suture, when the latter is present. In the Gerridae the true prescutum was found to be defined only in *Ptilomera* (fig. 72). The area bounded laterally by the parapsidial sutures is labelled the scutum (fig. 88). The scutoscutellar suture, which separates the scutum from the scutellum, is absent. The posterior region of the mesonotum continuous with the scutal region is thus labelled the scutellum (fig. 88). The postnotum is rather strongly drawn in, bearing the phragma beneath. Its posterior margin is nearly straight, with a small produced area at the middle. There is a narrow sclerite of unelucidated morphological significance along the scutellar region behind the tergal split, which Larsén (1945) called Gelenkkopf. The posterior margin of the postnotum is greatly produced medially in *Metrocoris* (fig. 76), nearly straight in *Ptilomera, Telmatometra, Rheumatobates* (figs. 72, 78, 80). Neither basalar nor a subalar sclerite is present. The longitudinal lateral membranous suture between the mesonotum and mesopleuron in the winged form is lost in winged forms in most species of Gerridae including *Gerris remigis.* The pits (fig. 88) on the posterolateral angles of the postnotum denote the presence of the phragma, which is less developed in the wingless forms than in the winged forms.

Heymons (1899*a*) observed that the tergum in Heteroptera develops from paired anlagen. In the nymphs of many species of Heteroptera the thoracic terga are divided into two more or less well-defined lateral plates by a median longitudinal impression, and both plates become more and more fused together in the later stages of postembryonic development. In the Gerridae also each tergal plate is well defined by the median longitudinal impression, and this impression becomes increasingly obscure in the later stages of development, but the original impression is still retained in varying degrees as the longitudinal sutures on the pro-, meso-, and metanota in many species of the Gerridae. This suture is called the median longitudinal sulcus in this work.

The mesosternum is indistinguishably fused with the mesopleural region in a majority of species of the Gerridae, but the suture separating the mesosternum from the mesopleuron is distinct in such a primitive genus as *Eotrechus* (fig. 86). The suture, when complete, leads posteriorly to the point of origin of the mesosternal apophysis. The mesocoxal (supracoxal) cleft, or mesoacetabular cleft (fig. 93) extends considerably forward in all species of the Gerridae. The second phragma (figs. 89, 90) in the winged form is well developed and laterally connected with the bases of the mesothoracic sternal apophyses; the posterolateral arms of the phragma in *Metrocoris* however, in the absence of the mesothoracic sternal apophyses, are attached to the inner dorsal angle of the mesoacetabula.

The wing base (figs. 84, 85): In the forewing the first axillary sclerite is articulated with the anterior notal process which is the anterior lateral angle of the tergal split; the second axillary sclerite is located along the first axillary sclerite; the third axillary sclerite is articulated with the acute base of the wing below the anal fold; the median plates are obscurely defined. The tegula is absent. In the hind wing the axillary sclerites are more reduced. The first axillary sclerite is located along the anterior notal process (Gelenkkopf of Larsén, 1945). The individuality of the other two sclerites are also maintained; the median plate with its proximal margin darker. Neither the humeral plate nor the tegula is recognized.

The wing venation: For the naming of the forewing venation I have followed Hungerford and Matsuda (1958a). In fig. 83 R + M and Cu are fused basally, separated into R + M and Cu, respectively, beyond the middle of the forewing. The former, in turn, branches into R and M, respectively, of which R is united with Sc by an oblique vein Sc_2; Cu is apically joined by the vein A and further with M. A is connected with the lower margin of the wing by a short cross vein. In the hind wing (fig. 82) R + M and Cu are clearly separated basally. Cu is apically joined with M. Cu and A are not joined together apically.

The metathorax

(Figs. 72-81, 86-90)

The metanotum in the winged form is defined laterally by the longitudinally elevated carina (fig. 88). This carina probably contains at least partly the element of the first abdominal segment, since the carina is continuous from the abdominal connexivum. The anterior encroachment of the first abdominal segment is also most clearly seen in Rhagadotarsinae (fig. 97), in which the true first connexival segment reaches the definitive intersegmental suture between the mesonotum and metanotum. In the Veliidae also, Esaki and Miyamoto (1955) have shown that the so-called metanotal triangle is actually the first abdominal pleurite. The encroachment of the pleurite of the first abdominal segment into the metathoracic region is thus a fairly common feature in the Gerroidea. In some groups of the Gerridae the first abdominal tergite has its anterior margin straight and the metanotum does not appear to contain the element of the first abdominal segment, as will be discussed in the next chapter. The metanotal longitudinal sulcus is shown in fig. 88. The third phragma does not occur in the Gerridae. The metathoracic spiracle is conspicuous, placed cephalo-caudad, occupying the intersegmental position between the mesonotum and metanotum laterally.

There occur two sutures in the metapleural region in the Gerridae. The one is the primary intersegmental suture between the meso- and metanota which goes in line with the metathoracic spiracle laterally. Another suture goes dorsally behind the metathoracic spiracle, and this suture is here called the metacetabular suture. The metacetabular suture occurs in the metapleural region, but this suture is definitely not homologous with the pleural suture in lower pterygote insects which leads dorsally to the wing base. This suture is dorsally connected with the posterior margin of the mesonotum in some groups of the Gerridae. Matsuda (1957) called this composite suture "the secondary intersegmental suture." More detailed investigation in this work has revealed more information about the nature of the definitive intersegmental suture between the mesonotum and metanotum occurring in the Gerridae. Comparing the tergum of the winged form and that of the wingless form of *Ptilomera* species (figs. 72, 73) it becomes immediately obvious that the intersegmental suture between the meso- and metanota in the wingless form very likely represents the posterior margin of the postnotum in the winged form dorsally; laterally the suture goes anteriorly then again posteriorly to the metathoracic spiracle, which is located on the intersegmental region between the mesothorax and metathorax. The intersegmental suture in the wingless form of *Ptilomera* is thus the veritable intersegmental suture and it is complete dorsolaterally. In *Gerris remigis* (figs. 74, 75) the intersegmental suture in the wingless form apparently corresponds to the posterior margin of the mesothoracic postnotum dorsally; laterally the suture is directly connected with the conspicuous metathoracic spiracle which is located more dorsally than in *Ptilomera.* In *Metrocoris ståli* (?) (figs. 76, 77) the definitive intersegmental suture appears to represent the posterior margin of the scutoscutellum, instead of the postnotum, dorsally. The suture defining the greatly produced postnotum in the winged form, by all criteria, seems to have been lost in the wingless form. In *Telmatometra whitei* (figs. 80, 81) apparently another kind of combination of sutures is responsible for the production of the definitive intersegmental suture in the wingless form. It is noticed that the postnotum in the winged form is large and subquadrangular in shape, its posterolateral angles are closely approximated to the dorsal end of the metacetabular suture. From this condition in the winged form it will be a simple step for the metacetabular suture to become connected with the posterolateral angle of the postnotum in the wingless form, thereby producing the nearly straight, long dorsal margin of the definitive intersegmental suture between the meso- and metanota. For the production of the definitive intersegmental suture in *Rheumatobates crassifemur* the same combination of the sutures most probably are involved, as will be understood by comparing figures 78 and 79 with 80 and 81. There are thus three different kinds of definitive intersegmental sutures in the wingless forms of the Gerridae. Behind the metathoracic spiracle the metacetabular suture is internally marked off by the carina (Pleuralintersegmentalhaken (Larsén, 1945), which leads internally to the base of the mesosternal apophysis (fig. 93).

The metasternum in *Gigantometra gigas* (fig. 87) is provided with the median unpaired omphalium and the lateral groove leading laterally to the opening on the metacetabula; the opening is covered with a tuft of hairs; the median omphalium is retained in many genera, but the lateral groove is lost in most genera of the Gerridae

The supracoxal cleft does not occur in the metathorax. The basal part of the coxa is inserted beneath the supracoxal lobe. The basal margin of the coxa is oblique in all legs. The paracoxal sclerites are above the ventral and dorsal basal margins of the coxa and thin membrane is attached to each sclerite (fig. 91, 92). The anterior tip of the middle coxa is articulated with the base of the supracoxal cleft and two small black sclerites are loosely connected to each other. The trochanter is narrow and elongate; the trochanteral apodeme bears a large thin membrane for the attachment of muscles, and is present in all legs.

The abdomen

The pregenital segments

(Figs. 94-106)

One of the peculiarities of the hemipterous abdomen, according to Heymons (1899a), is the progressive loss of the pleural element during the embryonic development. The tergite and the sternite become fused and the spiracle, which was originally in the pleural region, becomes located in the sternal region. In addition to this peculiarity, the fused plate, which is composed primarily of the tergite and sternite, has a tendency to produce a secondary lateral division by sutures either dorsally or ventrally or both. Heymons called the secondarily divided lateral region the paratergite, and the ventral plate the parasternite respectively.

1. *The first abdominal segment.*

The first abdominal segment is dorsally clearly retained in all species of the Gerridae. The entire (*i. e.* not laterally obliterated) anterior margin of the first abdominal tergite is present in some groups of the Gerridae. In *Brachymetra* (fig. 527), for instance, the anterior margin of the first tergite is horizontal, meeting with the anterolateral angle of the first definitive connexival segment, embracing the spiracle behind at the anterolateral angle of the first tergite; the spiracle is also bounded by an oblique suture which reaches the middle of the anterior margin. In some other groups of the Gerridae the anterior margin of the first tergite is bisinuate and laterally not reaching the anterior end of the first connexival segment (*e. g. Gerris*, fig. 95). The lateral longitudinal ridge (suture) of the metanotum in fig. 95 is probably partly the first segment (pleurite) as discussed previously. It should be noted that in *Brachymetra*, in which the connexivum is anteriorly defined by the straight anterior margin, no such ridge occurs in the metanotal region. The first segment is always completely lost ventrally except for the Rhagadotarsinae. Lundblad (1933) has already noticed this fact. Matsuda (1957), however, identified the anterior margin of the first ventrite in *Rhagadotarsus* (fig. 96) as the omphalial groove leading to the metacetabular region, chiefly because of the preconception that the first abdominal segment is always incorporated ventrally into the formation of the metasternal wall of the coxal cavity in Heteroptera. I now think this interpretation is wrong on the basis of the following evidence: (1) the first abdominal pleurite is distinctly incorporated into the metathoracic region; (2) the median omphalium is absent in Rhagadotarsinae; (3) there is at least no lateral opening of the omphalial groove on the metacetabular region, although the opening is obliterated in some forms of Gerridae in which the omphalial groove occurs. The Rhagadotarsinae is a quite abnormal group of the Gerridae combining highly specialized with highly primitive characters, as will be pointed out in the next chapter.

2. *The second to seventh abdominal segments.*

The connexivum is the paratergite dorsally and the parasternite ventrally according to Heymon's findings (1899). The connexivum is dorsally well defined by the longitudinal suture from the tergal region. The connexivum is always present in the second to the seventh segment but is never present in the eighth segment; in Rhagadotarsinae it is clearly present in the first segment. Ventrally the connexivum (parasternite) appears to be defined by the longitudinal suture which runs more ventral to the abdominal spiracle (fig. 94). The suture is more distinct and more complete in the primitive genera of the Gerridae, totally disappearing in some highly specialized groups. The seventh connexival segment is more or less greatly produced, forming the connexival spine (fig. 94). In many species of the Gerridae the ventral apical margin of the seventh segment is concave.

The genital segments

(Figs. 98-106)

1. *Origin of the male external genitalia in Hemiptera.*

Before describing the external genitalia of the Gerridae, it appears to be necessary to mention a recent development of opinions in regard to the origin of the external genitalia of insects, with special reference to Hemiptera. The external genitalia of insects are generally conceived to be the derivatives of the segmental limbs, that is, coxal in origin. Recently Dupuis (1950) elaborated a theory that the male genitalia of insects are derivatives of the tenth abdominal limbs. He coined the terms euphalic and pseudophalic organs, referring to the phalic organs including the parameres (tenth coxite) and to the structures from the ninth coxites respectively. He applied his theory to Heteroptera (1955). He disagreed with Bonhag and Wick (1953) who have shown that the male phalic organs arise from the ninth sternum in *Oncopeltus* (Lygaeidae, Heteroptera). Snodgrass (1957, December) indicated that the male insect genitalia including those of Heteroptera are the derivatives of the ninth sternum. Matsuda (1957 August, 1958 January) discussed the origin of the insect external genitalia in some detail and came essentially to the same conclusion as Snodgrass, but he credited the discovery to Heymons (1896-1899) who maintained the sternal origin of the external genitalia of insects over a half century ago. Woodland (1957, December) also has shown in his embryological study on *Thermobia domestica* that the external genitalia in this morphologically important species has nothing to do with coxites in their developmental origin.

As noted from the foregoing brief review on the recent development of opinion in regard to the origin of the external genitalia the overall indication is that the male external genitalia of insects are not the derivatives of the appendages. However, Dupuis' work (1955) is so important for hemipterists and so excellent in gathering the widely scattered information about the male genitalia of Heteroptera that his work, especially his basic concept in regard to the origin of the male genitalia, needs to be taken seriously. Dupuis (1955) refutes Bonhag and Wick's study by pointing out that "Ce point de vue conduit à une numérotation erronée des sternites postgénitaux (δ ci-après), se fonde sur une observation myologique dépourvue de signification (α) et sur une interprétation ontogénétique sans valeur (β) qui méconnait les faits essentiels de la morphogénèse des genitalia mâles des insectes (γ)."

As to (α) the myological evidence here at issue is the muscle of the stylus on which Bonhag and Wick relied for determination of the gonostylus. This muscle, in my experience also, is highly stable throughout many orders of insects and can be used as a good landmark in determining the stylus. As Dupuis states many muscles appear to be highly unstable in regard to their points of origin and insertion when we examine highly specialized forms of insects; but the musculature in lower groups of many orders maintains stable relationships as regards origin and insertion. This is what I have experienced in my studies of musculature associated with certain structures, such as the tentorium, the thoracic sternum, etc. The musculature can be a very important guide in morphological studies if the materials are carefully chosen and systematically studied in series of forms from more generalized to more specialized groups. If Dupuis' statement is generally true, morphology as a study of homology cannot exist.

As to (β), Dupuis believes that what Bonhag and Wick thought to be the ninth sternite is actually the tenth sternite on the ground that the larval structures do not necessarily coincide with the imaginal structures in location. This appears to contradict him in two ways. First, it should be remembered that his theory is based exclusively on the embryological evidence and on the data of postembryonic development of the male genitalia, which trace the development of the structures from stage to stage up to the adult.

If the larval (or nymphal) structures do not coincide with imaginal structures, how can his method of homology be justified? Secondly, even if the area which Bonhag and Wick observed to be the ninth sternite is actually the tenth sternite as Dupuis maintains, this sternite was observed to give rise to the male phalic organs. How can the sternite give rise to the male genitalia in Dupuis' theory?

As already discussed in detail by Snodgrass (1957) and Matsuda (1957, 1958), the theory which derives the male external genitalia from the tenth abdominal appendages is at least not well founded and it harbors many contradictions. Therefore, Dupuis' statement (γ) to the effect that Bonhag and Wick have misunderstood the essential facts of morphogenesis of the male genitalia is not valid.

Although Bonhag and Wick's study almost convincingly shows that the ninth sternite gives rise to the male genitalia, Qadri's study on the innervation of the genitalia in *Dysdercus* (1949) shows that the tenth abdominal nerves innervate the accessory gland, the median ejaculatory duct, and the intromittent organ. In *Dysdercus*, however, all the thoracic and abdominal ganglia are fused, forming a ganglionic mass in the thoracic cavity, so that the result is not highly reliable. The study of innervation is important in deciding segmentation but it will become reliable only by studying the series of forms from less specialized (less number of fused segmental ganglia) to more specialized. In Neuroptera the anterior seven abdominal ganglia are clearly separated from each other and only the ganglia from the eighth segment on are fused. This is the most generalized condition known in adult pterygote insects. Neuroptera will be the most suitable for this purpose as the basic material to work on.

In any case while the sternal origin of the male genitalia is well supported by evidence, it is less conclusive as to whether they are derived from the ninth or tenth segment. In this work Bonhag and Wick's finding and interpretations are provisionally followed.

2. *The male external genitalia of the Gerridae.*

Following Bonhag and Wick, the pygophore (figs. 98, 100) is the fusion product of the ninth coxites, and it covers ventrolaterally the genital chamber, enclosing the invaginated phallic organs. The pygophore is dorsally fused at its base, forming a narrow sclerotized bridge. The suranal plate (fig. 100) is usually considered to be the tenth segment or the tenth tergum by morphologists (Peytoureau 1895, Heymons 1899, Ekblom 1926 etc.) as well as by taxonomists. Bonhag and Wick, however, found this to be the ninth tergum in *Oncopeltus.* One great advantage attached to Bonhag and Wick's interpretation is that it is the ninth tergite in the male that bears apically the anus, and this is the condition in the female in the Gerridae. Thus, if we follow Bonhag and Wick, the homology of the genital segments between the two sexes becomes much easier than in the other theories. Although more studies, with this particular problem in mind, are necessary to either prove or disprove Bonhag and Wick's findings, their interpretation is followed in this work and so labelled.

The male phallic organs of the Gerridae were studied by Poisson (1922, 1924) Singh-Pruthi (1925), Ekblom (1926), Schroeder (1931), etc. Dupuis' excellent summary of the male genitalia in various groups of Herteroptera (1955), apart from its theoretical aspect, is also very useful.

The basal plate is attached laterally to the pygophore, sustaining the phallotheca within the genital chamber. The parameres arise from the point of connection of the basal plate to the pygophore. The phallotheca lies in the genital cavity with the basal end caudad and resting on and partly surrounded by the basal plate. During the copulation the phallotheca is raised and pushed backward then down, transcribing almost a complete circle. The phallotheca of Gerroidea is peculiar in that it contains the invaginated endosoma within. The endosoma is further divided into the proximal and distal membranous segments, and the conjunctiva between the two. In the resting position the phallotheca surrounds and encloses the endsoma and conjunctiva, its base attached to the basal plates and communicating with the body cavity through the basal foramen. The phallotheca is usually somewhat barrel-shaped, open at the distal end, through which the endosoma is extruded. The conjunctiva joins the phallotheca to the endosoma, being connected with the distal end of the former and the basal part of the latter. In the resting position it serves as lining between the two, and is turned inside out; the distal segment of the endosoma is usually provided with three pairs of sclerotized plates. They are (1) the median dorsal plate; (2) the ventral plates, and (3), the lateral plates. The median dorsal plate appears to be the fusion product of originally paired plates; the ventral plates appear to carry the ejaculatory duct. The number of plates are reduced in some groups of Gerridae, due to loss and fusion of plates.

3. *Origin of the female external genitalia in Hemiptera.*

As Matsuda (1958) pointed out, Christopher and Cragg's study on the development of the female genitalia in *Cimex* (1922) very convincingly supports the view maintained by Heymons (1896-1899) that the gonapophyses arise from the primary sternum. The study also supports Matsuda's contention (1957, 1958) that the valvifer is the modified sternum. Gillet's observation (1935) on the postembryonic development of the genitalia in *Rhodnius* and Rawat's observation (1939) on the development of the genitalia in *Naucoris* clearly indicate that a pair of buds arise on the eighth and ninth sternites. Each pair differentiates into outer and inner pairs, the inner pair on the eighth segment developing into the first valvulae, while the outer pair remains and forms only the first valvifers. The inner pair of buds on the ninth segment develops into the second pair of valvulae, while the outer pair develops into the third pair of valvulae and their bases form the second valvifers. These structures, however, are *theoretically* the gonocoxites of the eighth and ninth segments of Rawat. They can, however, also be the sternal structures as Christopher and Cragg's more detailed study on *Cimex* indicates. As far as embryological evidence indicates (Heymons, 1899a), there occur no embryonic abdominal appendage rudiments which might give rise to the external genitalia in *Nepa, Notonecta, Cimex,* and *Pyrrhocoris.*

It is clear from the foregoing discussion that there is no factual evidence whatsoever which supports the theory of the appendicular origin of the female genitalia in Heteroptera. The valvulae and the valvifers in *Rhodnius* and *Naucoris* studied by Gillet and Rawat should be regarded as sternal structures.

4. *The structural plan of the female genitalia in Hemiptera, with special reference to the Gerridae.*

Snodgrass (1933) summarized the basic structural patterns of the female external genitalia of Hemiptera. Certain parts of his summary important to our study are given here:

(1) The shaft of the ovipositor is formed of the first and second valvulae, the first being external and ventral, the second internal and dorsal. The second valvulae are generally united with each other, either for a part or for most of their length.

(2) The first valvifers have a pleural position below the tergum on the sides of the eighth segment, though their posterior angles

may be flexibly attached to the ninth tergum. The dorsal muscles of the first valvifers arise on the eighth tergum.

(3) The first valvulae have each two proximal rami. The outer ramus is flexibly attached to the ventral angle of the first valvifer; the inner ramus expands in a small plate solidly united with the anterior ventral angle of the ninth tergum.

(4) The ninth tergum is exposed, and usually large. Its anterior ventral angles are produced forward as extensions to which are united the inner rami of the first valvulae.

(5) The second valvifers have a pleural position on the sides of the ninth segment beneath the lateral margins of the ninth tergum. Each is movably articulated with the tergum at the point near the middle of its dorsal margin.

(6) The second valvulae are attached proximally, each by a single arcuate ramus, to the anterior end of the second valvifer, and the ramus slides on the concave margin of the inner ramus of the corresponding first valvula.

(7) The third valvulae are well differentiated from the second valvifers; they form a pair of lobes ensheathing the distal end of the shaft of the ovipositor; rarely they are absent.

Among the species of the aquatic Hemiptera examined in this study, *Salda* sp. and *Mesovelia mulsanti* have structural plans closer to the above general structural plan in Hemiptera outlined by Snodgrass than the other species. In *Mesovelia mulsanti* (fig. 105) there occurs clearly the second valvifer and the third valvula, but they are absent in the great majority of the Gerridae, as typically seen in *Gerris remigis* (fig. 106). In *Gerris remigis* the first valvula is divided into the inner shorter and the outer longer lobes, the base of the outer lobe being directly connected with the first valvifer, which is a broad sclerite exposed behind the seventh sternite. The thick and membranous ramus, arising from near the apex of the outer lobe, goes cephalad then turns again caudad to be indistinguishably fused with the process of the ninth tergite. The ramus is distinct from the process by different degrees of pigmentation in some species of Gerridae and in *Mesovelia mulsanti* (fig. 105). The vulva is located between the inner lobes of the first valvulae. The second valvulae are connected by the interval-vular membrane, the apical margin of which is approximated near the apices of the second valvulae, while the ramus of the second valvulae arises along the inner margin of the second valvula near its apex, goes cephalad and turns laterally along the inner margin of the ramus of the first valvula. The apical end of the ramus is loosely attached to the inner margin of the ramus of the first valvula due to loss of the second valvifer. In some groups of Hemiptera including *Mesovelia mulsanti* the distal end of the ramus of the second valvula is attached to the base of the second valvifer, which bears apically the third valvula.

EVOLUTION OF STRUCTURES

In this section the evolution of each structure is discussed together with its taxonomic significance. While this section is devoted primarily to the study of structural evolution itself at the level above species, it has a secondary purpose to give reasons why I think certain characters are primitive or specialized. A list of characters with their primitive and specialized alternatives thus decided is given at the end of this section. This list of characters is in turn used in tabulating the characters in each group in the following section (classification) by referring to the number for each character in the list. Sometimes recourse was taken to a circular reasoning in deciding primitive or specialized alternative for a character. That is when its alternative, whether primitive or specialized, cannot be decided on morphological bases the decision was made only by its association with other primitive or specialized characters. For instance, when the short pronotum occurs consistently in relatively specialized species or genera the short pronotum is regarded as a specialized, reduced condition. For these characters a symbol (*) was put in the list of characters.

I. EVOLUTION OF THE STRUCTURES OTHER THAN THE LEGS AND ANTENNAE

The shape of the body

In the subfamilies which are subsequently shown to be generalized, such as Gerrinae and Ptilomerinae, the shape of the body is elongate; it is shorter and rounder in more specilized subfamilies such as Halobatinae and Trepobatinae. That the primitive gerrids must have been elongate is convincingly evidenced by the fact that the shapes of the bodies of the structurally very primitive existing genera, *Eotrechus* and *Gigantometra,* are strongly elongate. The shortening of the body appears to have been brought about primarily by the reduction of the metasternum and abdomen. In *Eotrechus* the mesosternum is only about one and a half times as long as the metasternum. In *Gigantometra* and a few other primitive genera of Gerrinae the mesosternum is about twice as long as metasternum and relatively longer than in the other genera of the Gerridae. The extreme reduction of the metasternum is seen in the Halobatinae, in which the metasternum is represented merely by a subtriangular plate which usually does not even reach the metacetabular region.

In *Eotrechus, Gigantometra,* and larger species of some other primitive genera of Gerrinae, the abdominal segments are long and the second to seventh segments are subequal in length to each other; slightly more reduced abdominal segments are seen in the more specialized genera of Gerrinae, Ptilomerinae and in *Rhagadotarsus* of the Rhagadotarsinae; the strongest reduction of abdominal segments is evident in Trepobatinae, Halobatinae, and a few highly specialized genera of Gerrinae such as *Amemboa, Platygerris,* etc. In these groups the seventh and sixth segments together are often much longer than all the preceding segments together, due to shortening of the more anterior segments.

In the *Limnometra-Tenagogonus s. str.* complex of Gerrini, *Limnometra* is definitely longer than *Tenagogonus s. str.;* in *Gerris* the subgenus *Aquarius,* which is more primitive in the abdomen, is also definitely longer than *Gerris s. str.;* in the *Limnogonus s. str.-Limnogonellus* complex, the former is longer than the latter. In all these groups the metasternum and abdominal segments are relatively longer in subgenera of larger size. Noteworthy also is the fact that *Gigantometra* is relatively longer in the metasternum and abdominal segments than other genera within the tribe Gerrini, and it is the largest species in the Gerridae. In the Charmatometrini, *Charmatometra* has a relatively longer metasternum and abdominal segments than *Brachymetra,* which is structurally less primitive. In the Eotrechini the most primitive genus, *Eotrechus,* has relatively longer metasternum and abdominal segments than the other genera. In the smallest genus (in body length), *Amemboa,* the metasternum as well as most pregenital segments are greatly reduced in length. In the Cylindrostethini the length of the body has become progressively shorter in a phylogenetic series of *Cylindrostethus, Potamobates,* and *Platygerris,* and this is beautifully correlated with reduction of the metasternum and abdominal segments.

In the Halobatinae the metasternum has already been greatly reduced as mentioned previously, but it reaches laterally to the metacetabular region in the marine tribe Halobatini and it does not do so in the fresh-water tribe Metrocorini. The abdomen also has been greatly reduced. Thus, there is no striking difference in body length among genera of the subfamily, but if one compares two related genera, *e. g.*, the larger *Ventidius* and the smaller *Esakia*, it can be seen that reduction of abdominal segments is generally responsible for the shortness of *Esakia.*

Also in the Trepobatinae, the metasternum and abdominal segments are strongly reduced although to a lesser extent than in Halobatinae, and in Trepobatinae there is no striking difference in length among genera. In the related but structurally more primitive subfamily, Rhagadotarsinae, the metasternum and abdomen are relatively longer and the first abdominal segment is ventrally retained, and the subgenus *Caprivia* of the genus *Rhagadotarsus* is longer than any species of Trepobatinae. *Rhagadotarsus*, especially the subgenus *Caprivia*, is longer than *Rheumatobates* of the same subfamily which is structurally much more specialized. In the Ptilomerinae, *Ptilomera*, which is relatively large in size, has generally longer abdominal segments than in the other genera.

It is apparent from the foregoing discussion that among related genera of Gerrinae the reductions in lengths of the metasternum and pregenital segments are responsible for diminution of the body. In other subfamilies this is not so clear, but the smaller size in Trepobatinae and Halobatinae has evidently been brought about by the same mechanism. In these subfamilies the reductions of the metasternum and abdominal segments have reached their functional maximum. The same tendency at the species level is also clearly seen within most genera of Gerrinae if one arranges the species from larger to smaller size.

Concomittant with the reductions in lengths of the metasternum and abdomen, the body becomes relatively widened in the more specialized groups. A conspicuous example is the *Cylindrostethus-Potamobates-Platygerris* series. *Platygerris*, though presumably derived from a *Potamobates* like ancestor, is flattened and wider in shape. Another example is the *Ventidius-Esakia* complex. *Esakia* is generally considerably shorter than some species of *Ventidius*, and the body is more flattened. In Rhagadotarsinae the body is nearly cylindrical in the subgenus *Caprivia* of *Rhagadotarsus* and the hind coxae are so approximated to each other that they are not visible dorsally, but they are visible dorsally in *Rhagadotarsus s. str.* and *Rheumatobates* which are structurally more specialized as well as shorter and wider in the general shape of the body. All species of Halobatinae and Trepobatinae are much rounder and rather constant in shape, and much shorter than the species of Gerrinae and Ptilomerinae. It is interesting to call attention in this connection to a well-known classical example given by D'Arcy Thompson (1917), who has ingeniously shown that the sun-fish *Orthagoriscus* is a close relative of such elongate types as *Diodon* by applying the principles of Cartesian-co-ordinates. The great difference in general shape of the body between *Cylindrostethus* and *Platygerris,* for instance, must have been brought about by the same mechanism, *i. e.,* alteration in the anteroposterior growth gradient along the body axis.

Accompanied by the formation of the rounder general shape of the body in the higher subfamilies, the middle and hind leg bases have become more and more widely separated. A conspicuous example is seen in the *Rhagadotarsus*(*Caprivia*)-*Rhagadotarsus* (*Rhagadotarsus*)-*Rheumatobates* series, as noted previously. Obviously, the leg bases are much more widely separated from each other in the shorter and rounder Trepobatines and Halobatines than in the species of Gerrinae and Ptilomerinae. Probably the more lateral location of the leg bases have been favored by natural selection, since with more laterally placed leg bases more efficient locomotion on water might have become possible.

Certain deviations from the above mentioned general trend should be noted. In the marine Halobatinae, *Asclepios* and *Halobates,* the body size is evidently smaller in the structurally more primitive genus, *Asclepios,* than in *Halobates;* in *Ptilomera* also the structurally more primitive subgenus, *Proptilomera,* is smaller than in the more specialized subgenus, *Ptilomera s. str.* At the species level structurally (especially appendages and antennae) less specialized species are smaller than the more specialized species in *Rheumatobates.* In *Gerriselloides* the body length is about as long as one of the shortest species of closely related, more specialized *Gerris. s. str.*

Bianchi (1896) divided the Gerrinae into two subfamilies based on the general shape of the body. These were the Gerrinae, for genera with elongate bodies, and the Halobatinae, for those with shorter and rounder bodies. Actually highly specialized genera of Gerrinae (*Platygerris* and *Amemboa*) are shorter than related more primitive genera and have been placed in the Halobatinae, but they are structurally good gerrines, showing that Bianchi's criterion does not hold.

The head

The shape of the head: In the more primitive subfamilies such as Ptilomerinae, Gerrinae, and Rhagadotarsinae, the anterior margin of the head is not smoothly rounded in dorsal view. This is due to the projection of the clypeal region forward, to the well-developed maxillary plates, and to the well developed antenniferous tubercles laterally. In these groups the rostrum is not tightly appressed to the ventral surface of the head or to the prosternum, it is more or less free from them; the antennae tend to extend forward instead of ventrad in their resting positions. In the more specialized groups the clypeal region tends to be bent ventrally; the mandibular and maxillary plates tend to be fused, and the antenniferous tubercles become obsolete. Accompanying these changes, the rostrum tends to be less free from the ventral surface of the head and prosternum or from the mesosternum; the position of the antennal cavities shifts increasingly ventrad and the antennae tend to be more closely appressed to the ventral surface of the body. This correlated shift of structures is seen at the level of all taxonomic units. In Ptilomerinae the clypeal region forms a rather conspicuous, medially produced region and the antenniferous tubercles are conspicuous developments which are divergent apically in most genera; in *Rheumatogonus*, however, the clypeal region is more strongly bent ventrad, the antenniferous tubercles are more reduced, and the anterior margin of the head, therefore, is much more rounded in dorsal view than in other genera. In the Gerrinae the clypeal region and the antenniferous tubercles are still well developed in dorsal view, and the antennae arise always from above the anterior margins of the eyes. In the Halobatinae the clypeal region and the antenniferous tubercles are slightly produced on the anterior margin of the head in the marine *Asclepios-Halobates* complex; in *Metrocoris* and *Eurymetra* and few other related genera, the anterior margin of the head is practically not at all produced medially. It is simply broadly rounded in dorsal view, but the antennal cavities still open above the anterior margins of eyes. In the *Ventidius* and *Esakia* complex, the shift of the positions of the antennal cavities is beautifully seen in a series from *V. malayensis* to *E. kuiterti* (see figures 822, 823, 858). *Ventidius malayensis* is the largest species, and structurally more primitive than others. In this species the antennal cavities are clearly above the eyes, while in *V. kuiterti* the cavities are on the line across the anterior margins of the eyes. In *E. kui-*

terti, the cavities are below the anterior margins of eyes. The antennae and the rostrum in *Esakia* are closely appressed to the ventral surface of the body when they are at rest.

In all genera of Trepobatinae the anterior margin of the head is more or less smoothly rounded. The antenniferous tubercles are a little more developed in *Metrobates* than in others; the antennal cavities open just above the anterior margin of the eyes to a point a little below them. In Rhagadotarsinae the shape of the anterior margin of the head is rather strikingly different from the others. The antenniferous tubercles are conspicuously developed in the subgenus *Caprivia* of *Rhagadotarsus;* in *Rhagadotarsus s. str.* the structures are less pronounced, and are even much less developed in *Rheumatobates.* In all genera of Rhagadotarsinae the antennae arise from above the eyes, although one sees a continual reduction of the antenniferous tubercles from *Caprivia-Rhagadotarsus s. str.* to *Rheumatobates.* In this subfamily the mandibular and maxillary plates are clearly separated and the latter are so well developed as to form the bucculae, as in some more generalized terrestrial Heteropterons. These bucculae are clearly produced on either side of the clypeal region; the development of the bucculae is strongest in *Caprivia* and weakest in *Rheumatobates.* The clypeal region always projects forward as a median process of the head and the clypeus is basally well defined. The shape of the head in this subfamily is, thus, more like that of generalized Heteroptera and is the most primitive found among the subfamilies of Gerridae.

As the shape of the interocular space is directly associated with the shapes of the inner margins of eyes, it will be discussed in relation to the shape of eyes.

The eyes: In the primitive gerrids the eyes were probably indented, more or less globular in shape, relatively small, and not or but little covering on the anterolateral angles of the pronotum as is evidenced by the prevalence of this type of eyes in Ptilomerinae and in the majority of genera of Gerrinae. The eyes appear to have lost indentation and to have become larger and more laterally located, covering a great part of the anterolateral margin of the pronotum, in the more specialized subfamilies, Halobatinae and Trepobatinae. Evolution of the shape and position of the eyes is seen in the series from *Metrocoris* to *Esakia* (figs. 778, 822, 823, 858). In the Gerrinae, *Amemboa* and *Platygerris* have less indented eyes than their more primitive relatives, *Onychotrechus* and *Potamobates* respectively.

The shape of the interocular space of the head is directly dependent upon the shape of eyes. In the species in which the eyes are indented the interocular space is more or less strongly widened posteriorly. This is true of all genera of the Ptilomerinae, and a majority of genera of Gerrinae. The interocular space in Halobatinae and Trepobatinae is considerably less strongly widened posteriorly, due primarily to the absence of the ocular indentations.

As I have already pointed out (1957), the shape of the eyes has been erroneously considered to be a very important subfamily character by previous workers. Thus *Amemboa, Platygerris, Charmatometra, Brachymetra* and *Eobates,* because of their relatively short bodies and the shape of their eyes, have been placed in the Halobatinae. Because of the parallelism in evolution of eyes in this family, their shape cannot be used as a subfamily character. More fundamental morphological characters show that the five above-mentioned genera should be included in Gerrinae as will be more fully discussed elsewhere in this work.

The shape of eyes is much the same in the more primitive genera of Gerrinae, and is constant among all genera of Ptilomerinae, but is a character of specific rather than generic importance in the more specialized groups of the Gerrinae, Halobatinae, and Trepobatinae.

The clypeus: The basal margin of the clypeus is evident in the more primitive genera of all subfamilies, but cannot be seen in specialized genera of Gerrinae, Halobatinae and Trepobatinae. The anterior margin of the clypeus is more or less loosely connected with the labrum by means of membranous area. This condition is especially pronounced in the Cylindrostethini of Gerrinae. Whether the basal margin of the clypeus is retained or has been lost is usually generically constant.

The mandibular and maxillary plates, and the labrum: The mandibular plate is distinct from the maxillary plate in the more primitive genera of Gerrinae, Halobatinae, and Trepobatinae. In the Ptilomerinae and Rhagadotarsinae the plates are also quite distinct from each other. The maxillary plate has been discussed in connection with the shape of the head.

Whether the mandibular and maxillary plates are fused or not is usually generically constant. In Rhagadotarsinae the degree of development of the maxillary plate is somewhat significant at the generic or subgeneric level, and can be used as a taxonomic character at these levels. Externally the labrum does not provide any good taxonomic character at any taxonomic level.

The rostrum: The greater part of the rostrum consists of the third and fourth segments. Since these segments are easiest to measure, their measurements for all species available for study are given in table 16. It was found that there exists a strong tendency for the ratio of the third segment to the fourth to be greater in the more primitive and larger (in body length) genera than in related, more specialized smaller (in length) genera. This tendency is noted also at the species level within genera.

In Gerrinae the above tendency is noted in the *Aquarius, Gerris s. str.,* the *Limnogonus s. str.-Limnogonellus* complex, the *Limnometra-Tenagogonus s. str.* complex, *Eurygerris,* in the Eotrechini including four genera (*Eotrechus, Onychotrechus, Chimarrhometra,* and *Amemboa*), in the Cylindrostethini including three genera (*Cylindrostethus, Potamobates, Platygerris*) and in *Brachymetra.* In the Halobatinae the tendency is noted in the *Ventidius-Esakia* complex. In Trepobatinae the ratio of the third to the fourth segment is greater in *Telmatometra* and *Halobatopsis* than in the related and smaller (in length) genus *Ovatametra.* In the relatively primitive, but not the largest (in length) genus *Cryptobates* and *Telmatometra* the absolute length as well as relative length of the third segment is definitely greater than in any other genus of the subfamily. This indicates that these genera have a quite different growth pattern for the rostral segments from that of the other genera. In *Metrobates,* which is relatively large in size and primitive in structures, the relative length of the third segment is greater than in *Rheumatometra, Hynesionella, Metrobatopsis,* and *Naboandellus.* The length of the third segment in relation to the fourth segment appears to be directly correlated with absolute size in *Rheumatobates* and *Hynesionella,* in which the larger sex (female) has the third antennal segment relatively longer.

The above tendency must have been realized by the persistence of similar allometric growth patterns for these segments among related forms, in which the growth ratio for the third segment is greater than that for the fourth.

The prothorax

The pronotum: Prolongation of the pronotum in wingless forms is known to occur only in Reduviidae and Gerroidea in Heteroptera. In certain gerrids such prolongation does not occur in wingless individuals. That the lack of prolongation in wingless forms is a specialization is indicated by the following facts.

(1) Prolongation of the pronotum in wingless individuals occurs

in more primitive genera or subgenera of Gerrini, such as *Aquarius, Gerris s. str., Limnometra, Limnoporus, Limnogonus s. str., Tenagometrella,* etc., and the three genera of Charmatometrini.

(2) Varying degrees of reduction of the pronotum in wingless forms occur only in highly specialized species of some more specialized genera or subgenera of Gerrinae, such as *Limnogonellus, Eurygerris, Tenagogonus,* etc.

(3) In the genus *Rhagovelia* of the Veliidae, there occur varying degrees of prolongation of the pronotum; and the group with more prolonged pronotum in wingless forms has the more primitive wing venation in the winged forms.

If the lack of prolongation of the pronotum in wingless forms is a specialized condition as reasoned above, Lundblad's (1936) and Matsuda's (1956) opinions that this feature is primitive should be retracted. Whether the above view is valid for Veliidae in general can be determined only by more extensive study of this family.

A more detailed consideration of evolution of the pronotum in wingless forms of Gerrinae follows:

In Eotrechini the pronotum in wingless forms is not prolonged in any genus although we do not know whether the pronotum is prolonged or not in wingless forms of *Eotrechus,* since wingless forms of this genus have never been found. The lack of prolongation of the pronotum in wingless forms of the other three genera, however, does not contradict the above view that the prolongation is a primitive condition, since the three genera are structurally much more specialized than *Eotrechus.* In Gerrini various stages of prolongation of the pronotum are noted. In the large (in size) and structurally primitive genus, *Gigantometra,* the pronotum is prolonged in wingless individuals (Hoffmann, 1936); in *Gerris* the pronotum is prolonged in all species examined, but in *Gerrisella,* which is somewhat related to *Gerris s. str.,* the pronotum is not at all prolonged in wingless forms. In *Limnoporus,* which is relatively primitive and large in body size, the pronotum is prolonged in wingless forms. In the *Limnometra-Tenagogonus s. str.* complex, an unprolonged pronotum occurs only in the highly specialized species, *T. madagascariensis;* interestingly, however, the pronotum is highly modified apically in *fijiensis* from Fiji. The evolution of the pronotum in this genus has taken two quite different courses, one toward reduction in Madagascar and another toward further modification in the Pacific; in the related genus *Tenagometra* from

Africa the pronotum is not at all prolonged although in another related but relatively primitive genus, *Tenagometrella*, the pronotum is prolonged in wingless forms. In the *Limnogonus s. str.-Limnogonellus* complex there are seen varying degrees of reduction of the pronotum in wingless forms in the specialized, smaller (in size) subgenus *Limnogonellus*. In *Eurygerris*, there also exist varying degrees of reduction of the pronotum from the almost fully prolonged condition in *E. mexicanus* to highly reduced conditions in other species. No wingless forms of the genus *Tachygerris* have ever been recorded.

In Charmatometrini the pronotum is always prolonged. In Cylindrostethini and all other subfamilies of the Gerridae the pronotum is not prolonged in wingless forms.

Prolongation of the pronotum in wingless forms is a tribal character in Gerrinae except for Gerrini. Since there is a clear indication that the pronotum is in the evolutionary process of progressive reduction independently in various groups of Gerrini, this cannot be used to define natural groups in that tribe, but can be a good species character. Sometimes the color of the longitudinal stripe is a good generic character, *e. g.*, in *Tenagometrella* the pronotum has a median yellow longitudinal stripe instead of a black stripe as in related genera; in *Limnogonus* the pronotum always has a yellow stripe on the apical margin; etc. In the winged forms the shape and the position of the humeri are of taxonomic importance, *e. g.*, the relatively caudal position of the humeri is characteristic of Cylindrostethini.

The Mesothorax

The lateral longitudinal suture of the mesothorax: The lateral longitudinal suture separating the mesonotum from the mesopleural region is retained in the Rhagadotarsinae, *Potamometra* of the Ptilomerinae, and *Tenagogonus (Tenagometra)* and *Eurygerris* of the Gerrinae in which the pronotum is not prolonged in wingless forms. The suture is completely lost in the other two subfamilies. When this suture is clearly retained it constitutes a good generic, subgeneric or subfamilial character.

The median longitudinal sulcus of the mesonotum: This suture, as already indicated, is the exuvial suture. When present, therefore, this is a nymphal character. It is highly conspicuous and represented by a longitudinal groove in females of *Rheumatometra* and *Rheumatometroides*.

The mesosternum: The mesosternum in more primitive genera of Gerrinae is provided with a pair of longitudinal sutures on either side of the median longitudinal axis. That these sutures are probably the ones separating the primary mesosternal region from the lateral mesopleural regions is supported by the facts that the sutures occur only in more primitive genera of Gerrinae and Ptilomerinae, or in more primitive species of some genera of Gerrinae. The sutures are distinct and extend through the entire length of the mesothorax, extending posteriorly to the bases of the sternal apophyses in *Eotrechus.* The sutures tend to become divergent and obsolescent posteriorly when they occur in other genera. The sutures are present in *Gigantometra,* all species of *Limnoporus,* in most species of *Aquarius* and *Gerris s. str.,* and in some species of *Onychotrechus, Eurygerris, Limnometra, Limnogonus,* and *Cylindrostethus.* They are distinct only anteriorly in *Limnogonellus* when they are present. Also they are distinct in some species of *Ptilomera* of Ptilomerinae, not recognizable in other genera of Ptilomerinae, and appear to have been completely lost in all other subfamilies.

The mesosternum is often impressed longitudinally on the anterior half of the median longitudinal axis. This suture is apparently a secondary depression to receive the apical portion of the rostrum. In the groups in which the rostrum is short, not extending beyond the prosternum (Cylindrostethini), the anterior margin of the mesosternum is either simply rounded or sometimes even strongly swollen and produced anteriorly at the middle. In females of *Heterobates* the mesosternum is provided with a median well-demarcated flattened area which extends posteriorly as far as the apical region of the abdomen. Other kinds of modifications seen in *Ventidius (Ventidiodes),* and *Metrobates* are described elsewhere. The mesosternum, located between the prosternum and metasternum, appears to have been least modified and least reduced in length during the course of evolution throughout the family.

The intersegmental suture between the mesonotum and metanotum: As the morphological study of this suture has revealed, the nature of the definitive intersegmental suture between the meso- and metanota differs rather widely in different groups of the family. It was also found that two different sutures are involved in the formation of the definitive intersegmental suture, *i. e.,* the primary intersegmental suture and the suture here called the metacetabular suture.

In figure 107 is shown the possible evolutionary history of the intersegmental suture in wingless forms of the Gerridae. In the hypothetical primitive gerrids the primary intersegmental suture is complete throughout the dorsolateral part of the body, as seen in some genera of Gerrinae and all genera of Ptilomerinae, and the metacetabular suture is only weakly developed dorsally. From this primitive condition the metacetabular suture became united to the anterolateral angle of the first tergite, while the primary intersegmental suture is retained laterally, as seen in Ptilomerinae. In Gerrinae the most primitive condition is seen in *Charmatometra,* in which the primary intersegmental suture is retained dorsolaterally and the secondary metacetabular suture is only weakly developed as in the hypothetically primitive gerrids. In the other two genera of Charmatometrini the primary intersegmental suture is often obsolete laterally. In Eotrechini the primary intersegmental suture is retained laterally and in Gerrini it is more or less obliterated laterally. The metacetabular suture is better developed than in Charmatometrini in these two tribes. From the sutures seen in Eotrechini the condition in Cylindrostethini must have been produced by complete fusion of the metacetabular suture with the dorsal margin of the primary intersegmental suture, while the primary intersegmental suture was still retained laterally. From the type of sutures in Cylindrostethini it is a simple step to produce the type of suture in Rhagadotarsinae and Trepobatinae with the complete loss of the prespiracular part of the intersegmental suture. The type of the sutures in Halobatinae has probably arisen from those in Gerrini by having the suture dorsally (which represents the posterior margin of the mesothoracic postnotum in winged forms) replaced by the posterior margin of the mesothoracic scutellum in winged forms.

The differences in the nature of the sutures are of great taxonomic importance at the subfamilial and tribal levels. The other characters correlated with the different types of the sutures further strengthen their taxonomic values. In fact all the genera included within each subfamily and tribe share very much the same sutures described above.

The metathorax

The metathoracic spiracle: The metathoracic spiracle is distinct in all species of all subfamilies, and located always anterior to the metacetabular suture. The orientation of the spiracle—whether it is cephalocaudally or nearly dorsoventrally oriented—is quite constant in each subfamily. In the subfamilies having the primary intersegmental suture between the mesonotum and metanotum more or less retained laterally, the spiracle is placed cephalocaudally. This orientation of the spiracle is seen in all species of Gerrinae, Ptilomerinae and Halobatinae without exception. In all species of the subfamilies in which the primary intersegmental suture is completely lost laterally (Rhagadotarsinae and Trepobatinae), the spiracle is oriented more nearly vertically, especially in Trepobatinae. Often the anterior end of the spiracle and the metacetabular suture are connected by a faint suture (figs. 80, 81) in Trepobatinae. This suture, in spite of its prespiracular position, is not homologous with the primary intersegmental suture, since it does not reach anteriorly to the wing base in winged forms.

As noted from the above description the orientation of the spiracle is highly correlated with the two fundamentally different types of the intersegmental suture, by which the Gerridae can roughly be divided into two major groups.

The median longitudinal sulcus of the metanotum: This occurs in most genera of Gerrinae, Trepobatinae, Rhagadotarsinae, and some genera of Ptilomerinae. It is the ecdyseal suture. The presence or absence of this suture is usually generically constant.

The lateral longitudinal ridge of the metanotum: The morphology of this ridge (sometimes a suture) has been discussed in some detail previously. It is obvious that the presence of this suture is secondary. In the Ptilomerinae, Charmatometrini, in which the nearly straight and complete anterior margin of the first tergite is retained, this secondary suture does not exist. The presence or absence of this secondary suture is thus correlated with the presence or absence of the straight, laterally unobliterated anterior margin of the first abdominal tergite. As already shown, this suture is especially well developed in Rhagadotarsinae, reaching clearly to the definitive intersegmental suture between the meso- and metanota. It is developed in varying degrees in Halobatinae, Trepobatinae, and Gerrinae except for Charmatometrini.

The metasternum: Since the mesosternum has apparently been least modified in length among thoracic segments during evolution, the relative length of the metasternum to the mesosternum should give a good criterion by which one can judge the degree of reduction of the metasternum. It was found in this study, by applying this method, that the degree of reduction of the metasternum is the least in *Eotrechus* in the Gerridae, in which the mesosternum is only about one and a half times as long as the metasternum; next are *Gigantometra* and *Cylindrostethus productus,* in which the mesosternum is a little less than twice as long as the metasternum, and the body size is very large and primitive structurally. In *Aquarius* and *Gerris s. str.* the relative length of the mesosternum to the metasternum is 2:1 to 3:1; in the *Limnometra-Tenagogonus s. str.* complex the mesosternum is three to almost six times as long as the metasternum; the metasternum in the larger species of *Limnometra* is relatively longer than *Tenagogonus s. str.* In the *Limnogonus s. str.-Limnogonellus* complex, also, the same relation holds; the mesosternum ranging from three to almost five times as long as the metasternum and being relatively longer in species belonging to the larger (in body size) subgenus *Limnogonus s. str.* than in the smaller *Limnogonellus.* In the Eotrechini the reduction of the metasternum has occurred progressively in the order of *Eotrechus, Chimarrhometra, Onychotrechus, Amemboa.* In the last genus the mesosternum is seven to ten times as long as the metasternum, and the body is the smallest. In the Cylindrostethini the metasternum has also become progressively reduced in the phylogenetic series from more primitive to more specialized, that is in the order: *Cylindrostethus, Potamobates, Platygerris.* In *Cylindrostethus* the ratio of the mesosternum to the metasternum ranges from 1.8:1 to 3.5:1, but it is about 10:1 in *Platygerris.* In the Charmatometrini the ratio is relatively constant, about 5:1 throughout the tribe.

In Ptilomerinae the degree of reduction of the metasternum is generally further advanced than in Gerrinae. The mesosternum is at least several times as long as the metasternum in all genera. In the Rhagadotarsinae the metasternum has not been much reduced; the mesosternum is only a few times as long as the metasternum in the great majority of species of the subfamily. In related subfamily Trepobatinae, the metasternum has been greatly reduced; the mesosternum is ten to twenty times as long as the metasternum in the great majority of the members of the subfamily; only in *Metrobates* is the mesosternum distinctly less than ten times as long as the metasternum. The extreme reduction of the metasternum is seen in Halobatinae, in which the metasternum is represented by a transverse subtriangular plate bearing the omphalium along its posterior margin, and this plate does not even reach the metacetabular region in Metrocorini, and barely reaching it in Halobatini.

Since the degree of reduction of the metasternum overlaps among related genera, it cannot be generally a diagnostic generic characters, but its highly reduced condition in Halobatinae is a good subfamily character as is its large size and anterior production in Rhagadotarsinae.

The omphalium: The omphalium and the groove leading from it onto the metacetabular region is retained in *Gigantometra, Gerrisselloides,* Charmatometrini, and Cylindrostethini of Gerrinae; the lateral groove is lost although the tuberculous omphalium is retained on the middle of the metasternum in all other genera of Gerrinae, Ptilomerinae, and Halobatinae. The omphalium, as well as the lateral groove, has been lost in Rhagadotarsinae and Trepobatinae except for *Rheumatometroides* and *Stenobates.* The presence of the omphalium and the lateral groove is the primitive condition as seen from the fact that they are retained in more primitive genera of each tribe of Gerrinae, although the groove is lost in *Eotrechus.*

The presence or absence of the omphalium and the groove leading onto the metacetabula offers an excellent generic diagnostic character in the Gerrinae. When only the median tuberculous omphalium is present, the location of the omphalium, whether it is close to or considerably away from the posterior margin of the metasternum, is generically often constant. Occasionally the shape of the omphalium, whether it is located on the more or less swollen surface or not, is a good species character (*e. g., Eurygerris*). The tuft of hairs which usually covers the lateral opening of the groove on the metacetabula varies in degree of development in various species and this may be a good species character. The total absence of the omphalium is a good subfamily character for Rhagadotarsinae.

The first abdominal segment

The first abdominal tergite: The lateral loss of the anterior margin of the first abdominal tergite must have occurred independently in some or all genera of all subfamilies. In Gerrinae the complete and nearly straight anterior margin is retained in the Charmatometrini; the definitive anterior margin of the first tergite in many genera of Gerrinae is laterally represented by an obscure secondary suture or depression running slightly behind the first abdominal spiracle and by the genuine suture running obliquely forward in front of the first abdominal spiracle, which does not reach anterolateral angle of the first connexival segment. The anterior margin of the first abdominal tergite in these forms is thus roughly flattened W-shaped or bisinuate (here secondary oblique lateral depressions are not considered). In Ptilomerinae the complete and straight anterior margin of the first tergite is clearly retained in both sexes of *Rhyacobates, Potamometroides, Rheumatogonus, Potamometra, Ptilomera* and *Pleciobates* (?). It is obliterated and modified in the females of *Heterobates* and *Potamometropsis,* and the tergite is medially curiously modified in the female of *Potamometra,* though the anterior margin is retained. In Halobatinae the anterior margin is retained rather clearly for its entire width in *Metrocoris* although it runs obliquely forward laterally in front of the spiracle; rather clearly retained laterally, though obliterated medially, in *Asclepios* and *Halobates;* in *Ventidius* and *Esakia,* especially the latter, the anterior margin is obliterated at least in wingless forms of most species. In the Rhagadotarsinae and Trepobatinae the anterior margin tends to be obliterated medially, and in some genera of Trepobatinae (*e. g., Cryptobates*) the anterior margin is even indistinct laterally or lost.

The connexival part of the first abdominal segment: The connexival part of the first segment is distinct from that of the second only in Rhagadotarsinae, in which the connexival part of the first segment encroaches into the lateral region of the metanotum. In the rest of the family the connexivum of the first segment is invariably fused with the second or sometimes indistinguishably fused with the second and third, and encroaches into the mesonotum (lateral longitudinal elevation) in varying degrees in various groups.

The first abdominal ventrite: The first ventral abdominal segment is clearly retained and even longer than the second ventrite in Rhagadotarsinae; in all other subfamilies the first ventrite is completely lost at least superficially, and the first clearly recognizable ventrite is actually the second ventral abdominal segment.

The combination of the characters found in the tergite, connexivum, and ventrite provides good generic or sometimes good subfamily characters. The degree of reduction of the anterior margin of the abdominal tergite, whether it is retained throughout the entire width or obliterated medially or laterally, or whether it is straight or flattened W-shape, etc., are generically constant for most genera, and often constant at the tribal and subfamilial levels. Whether the first connexival segment extends into the metanotal region or not is the character that distinguishes the clearly related genera, *Ventidius* and *Esakia.* The retention of the line separating the connexivum of the first segment from that of the second and the retention of the first abdominal ventrite are important subfamily characters of Rhagadotarsinae. Matsuda (1955) suggested the taxonomic significance of the basal abdominal tergites in Heteroptera in general; he (1956) also found that the varying degrees of modification of the basal tergites in the winged forms of *Rhagovelia* (Veliidae) serve as subgeneric characters. In the Gerridae the basal abdominal tergites, especially the first, provide important taxonomic characters at the subfamilial, tribal, and generic levels.

The second to sixth abdominal segments

The second to sixth abdominal tergites and ventrites: Like the mesothorax among the thoracic segments the second to the sixth segments, situated between the proximal and distal genital segments, have had the least modification in evolution. At least dorsally these segments are subequal in length in most genera of all subfamilies. In some genera of Trepobatinae (*Cryptobates,* some species of *Halobatopsis* and *Ovatametra*) and in some genera of Halobatinae (*Ventidius* and *Esakia*) the anterior margin of the second tergite is obliterated; in some genera of Ptilomerinae (*e. g., Heterobates*) the basal abdominal tergites are greatly modified due to strong reflection of the connexivum on the dorsum in the female; in *Potamometroides hoogstraali* the sixth tergite is provided with the median projection, also the apical angles of the sixth connexival segment in the female is strongly produced. In all other subfamilies the second tergite tends to be produced anteriorly on the anterior margin; this tendency is especially pronounced in Trepobatinae and Halobatinae.

Ventrally the second to sixth segments are subequal and relatively long in the more primitive genera of Gerrinae, such as *Eotrechus, Gigantometra,* most species of *Aquarius, Gerris s. str., Limnometra* etc. The segments ventrally are shorter than dorsally though still subequal in most genera of Gerrini. In Eotrechini the abdominal segments are greatly reduced ventrally in *Amemboa* and *Chimarrhometra;* among Cylindrostethini the posterior margin of the sixth ventrite in some species of *Potamobates* and all species of *Platygerris* is produced anteriorly at the middle in female. In Ptilomerinae the abdominal segments are more often not subequal to each other ventrally. The degree of reduction of the second to the sixth ventrites is generally greater than in Gerrinae; and in genera, in which a large part of the abdomen is telescoped within the thoracic cavity, the male abdominal ventrites are greatly reduced *(Potamometroides).* In the Rhagadotarsinae the second to sixth segments are relatively long and subequal in length both dorsally and ventrally in *Rhagadotarsus,* shorter but still subequal in length in *Rneumatobates.* In Trepobatinae the abdomen is as in *Rheumatobates* but at least the sixth segment is a little longer than the fifth segment in a great majority of species of all genera. In the males of *Metrobatopsis* and *Hynesionella* the degree of reduction of the abdominal segments is greatest in the subfamily. In Halobatinae a condition similar to that in Trepobatinae exists, the greatest degree of reduction of the second to the sixth ventrites having been attained in *Ventidius, Esakia, Halobates,* etc.

Location of the abdominal spiracles. There is a consistent tendency for the abdominal spiracles in more primitive species of more primitive genera to be located closer to the anterior margin than to the posterior margin of their respective segments. The spiracles are located more caudad, or even at the middle of the segments in more specialized species with more reduced abdominal segments within the same genus. This process of shift of the location of the spiracles is beautifully seen in such a diverse group as the *Limnometra-Tenagogonus s. str.* complex. In this group the spiracle is placed distinctly closer to the anterior margin than to the posterior margin in species with long abdominal segments. In *T. (L.) anadyomene* and in all species of *Tenagogonus s. str.* the spiracle is at the middle of each segment. A similar tendency is also seen in the *Cylindrostethus-Potamobates* series; in all species of *Cylindrostethus,* in which the abdominal segments are long, the spiracles are placed closer to the anterior margin than to the posterior margin of all segments, whilst in all species placed under *Potamobates* except for *P. thomasi,* in which the abdominal segments are shorter than in *Cylindrostethus,* the spiracles are placed at the middle of each segment, or even closer to the posterior than to the anterior margin; in *P. thomasi* the spiracles are placed closer to the anterior margins than to the posterior margins of abdominal segments, and the abdominal segments in this species are the longest among the species of *Potamobates.* A similar situation to those in the above mentioned genera is also seen in *Aquarius* and *Gerris s. str.* at the specific level. In the Charmatometrini the abdominal spiracles are placed closer to the anterior margin than to the posterior margin in *Charmatometra* and *Eobates,* but at the middle in most species of *Brachymetra.* The spiracles are also placed closer to the anterior margins than to the posterior margins in such primitive genera as *Eotrechus* and *Gigantometra,* but at the middle of each segment in *Tachygerris, Chimarrhometra, Platygerris, Onychotrechus* and probably

Amemboa (not examined), all more or less highly specialized genera of Gerrinae.

In the Ptilomerinae the spiracles are placed at the middle of each segment except for *Ptilomera,* in which the abdominal segments are relatively long and the spiracles are in front of the middle of the segments. In Rhagadotarsinae the fifth and sixth abdominal spiracles are located closer to the anterior margin than to the posterior margin of each segment in the subgenus *Caprivia* of the genus *Rhagadotarsus;* in *Rhagadotarsus (Rhagadotarsus)* and in *Rheumatobates* the spiracles are placed at the middle of their respective segments. In Halobatinae and Trepobatinae the abdominal segments are strongly reduced, moreover the basal areas of the metacetabula and the middle and hind legs are so superposed on the lateral region of the abdomen that it is usually very difficult to locate the spiracles under a binocular microscope, but whenever the spiracles are observed they are found to be located at the middle of each abdominal segment.

It is evident from the foregoing description that the primitive position of the abdominal spiracles in the Gerridae is closer to the anterior margin than to the posterior margin of each segment, and that the spiracles have had a tendency to shift their positions to the middles or even beyond the middles of the segments with progressive reduction of the abdominal segments.

The ventral longitudinal suture of the connexivum: The suture is most pronounced in more primitive species of the more primitive genera of Gerrinae in which the suture is only briefly broken at the middle of each segment. The suture extends almost the entire length of each abdominal segment, slightly mesad of the spiracle, but it becomes obliterated in more specialized species within the same genera or in more specialized genera of Gerrinae and is represented by two punctiform depressions. The sequence of obliteration of this suture is seen in such diverse genera of Gerrinae as the *Limnometra-Tenagogonus s. str.* complex, the *Aquarius-Gerris s. str.* series, the *Cylindrostethus-Potamobates* complex, etc. In *Gigantometra* the suture is well developed; in *Eotrechus* it is distinct but not as well pronounced as in *Gigantometra;* in the related but smaller and more specialized genus *Onychotrechus* it is indistinct; in such highly specialized genera of the subfamily as *Amemboa* and *Platygerris* it is very indistinct or completely lost; in the Charmatometrini it is either indistinct or lost. In the Ptilomerinae it is indicated by two oblique impressions mesad of the spiracle of each abdominal segment; it is most distinct in *Ptilomera* in which the abdomen is more generalized, indistinct or overgrown by silvery adpressed hairs in most other genera. In other subfamilies the suture is further obliterated and even completely lost; the two ill-defined shallow depressions mesal to the spiracle of each segment in *Rhagadotarsus* is probably the obliterated suture. In Halobatinae and Trepobatinae the suture is almost completely or completely lost.

The seventh abdominal segment

Theoretically, in primitive insects the seventh abdominal segment should be similar in form to the preceding segment. Search for this primitive condition in the Gerridae immediately encountered difficulty in that in no species of the Gerridae is the posterior margin of the seventh segment on the ventral surface straight as is the sixth. It is always either broadly concave or curiously modified, and often the seventh segment at the sides is strongly produced posteriorly as the connexival spines. Since the posterior margin is usually concave and the segment has a strong tendency to be produced laterocaudally, the relative length of the seventh to the sixth segment on the ventral surface is expected to be below 1 in primitive gerrids. It was found that this condition is seen in more primitive species of more primitive genera of Gerrinae, such as *Gigantometra, Eotrechus,* and more primitive species of *Aquarius, Limnometra,* etc. In these species the second to sixth abdominal segments are long and subequal to each other in length, and the lateral projections of the seventh are more or less conspicuous except for *Eotrechus.* In these primitive gerrids the seventh segment on its median longitudinal axis is about two thirds to three fourths as long as the sixth segment ventrally and the posterior margin is more or less strongly concave with resulting laterally produced area. From this primitive condition the seventh segment appears to have undergone various modifications in different groups.

The connexival spines do not occur in Eotrechini and Charmatometrini, but do occur in the more primitive species of the more primitive genera of Gerrini and Cylindrostethini. The absence of connexival spines in the more specialized genera of the latter tribe of the Gerrinae simulate the condition found, *e. g.,* in *Eotrechus.* In *Eotrechus,* however, the abdominal segments are generalized and long, while in the species without connexival spines in the Gerrini and Cylindrostethini the abdominal segments are strongly reduced.

The reduction of the abdominal segments are apparently correlated with progressive reduction of the connexival spines in Gerrini and Cylindrostethini. It is therefore likely that the connexival spines never occurred in the Eotrechini and probably also in Charmatometrini, and that the absence of the connexival spines in more specialized species of Gerrini and Cylindrostethini is due to secondary loss.

It is thus impossible to say simply that the absence or presence of the connexival spines is a primitive or specialized condition in the Gerridae; the absence or small size of the connexival spine in Gerrini and Cylindrostethini is evidently a specialized condition, but it is not necessarily so in the other two tribes. Possibly the most primitive condition is the absence of the connexival spines combined with a generalized abdominal form as seen in *Eotrechus;* this combination of characters has persisted in Eotrechini and Charmatometrini. After the acquisition of the connexival spines in the ancestral group of Gerrini and Cylindrostethini, however, the spines are again subject to loss.

The evolution of the seventh segment is somewhat different in the two sexes. The following descriptions are primarily at the subfamily level, and general problems, whenever encountered, are discussed here. More detailed discussion at the species level is given for each genus in the taxonomic section of this work.

The male: In Gerrinae the connexival spines occur in the *Limnometra-Tenagogonus s. str.* complex, in the *Limnogonus s. str.-Limnogonellus* complex, in *Aquarius, Limnoporus,* and in the *Cylindrostethus-Potamobates* complex. In these genera the connexival spines have become gradually obliterated with specialization of the abdominal segments. The prolongation of the seventh segment occurs, as in other subfamilies, in more specialized species of more generalized genera and in all species of more specialized genera. The degree of prolongation is indicated by the length of the seventh segment on the median ventral longitudinal axis in relation to that of the sixth segment. In the primitive Gerridae the median length of the ventral surface of the seventh segment is shorter than the sixth segment. The seventh segment has apparently become prolonged simultaneously with the reduction of the second to sixth ventral abdominal segments. This is seen at both the specific and generic levels within the subfamily Gerrinae. The greatest prolongation of this segment has been attained in *Amemboa, Chimarrhometra* and *Platygerris.* In *Aquarius, Gerris s. str.,* and in the

Cylindrostethini the ventral posterior margin of the seventh segment has become more and more emarginated at the middle with specialization (reduction) of the preceding abdominal segments. The two groups seem to share the same evolutionary potentialities in this respect and in retention of the connexival spines in more primitive species; in no other genera of Gerrinae does the median emargination on the ventral posterior margin occur. The process of modification of the seventh segment in the *Limnometra-Tenagogonus s. str.* complex is peculiar. In this group of subgenera the connexival spines also occur in species with more primitive abdomens. The spines are progressively reduced with specialization of the abdomen and become lost in certain highly specialized species. With further specialization of the preceding abdominal segments, there arise processes like the spines but more ventrally than the connexival spines. These structures migrate more and more ventrally and eventually are located near the median longitudinal axis of the abdomen.

In Ptilomerinae no conspicuous modification of the seventh segment has occurred in the males. The segment has been simply prolonged in more specialized species. The same applies to Rhagadotarsinae, Trepobatinae and Halobatinae. It should be noted, however, that in some species of Halobatinae a depression occurs on the basal region of the ventral surface, as in some genera of Gerrinae and Ptilomerinae.

The female: The connexival spines are more conspicuous in females than in males and are often retained in the female when they are completely lost in the male of the same species (*e. g.*, some species of *Limnometra, Gerris s. str., Tachygerris,* etc.). The reduction of the connexival spines is in general parallel to that of the males, but is in general less than in males in the Gerrinae. The seventh abdominal segment has undergone no conspicuous modification besides the prolongation of the segment itself and the reduction of the connexival spines.

The degree of specialization of this segment is thus well indicated, in most genera, by the length of this segment, especially its ventral surface, in relation to the preceding segment. In some highly specialized genera such as *Platygerris* and *Tachygerris,* however, the ventral apical margin of the segment has been greatly modified while still retaining the distinct connexival spines, and the eighth segment is incompletely concealed beneath this development of the seventh segment. In some species of *Eurygerris,* such as *E. car-*

iniventris, the seventh segment is so greatly developed ventrolaterally that the apical region of the connexivum simulates the connexival spines of the more primitive genera. That this is a secondary formation is convincingly evidenced by the fact that no such projection occurs in the more primitive species of the same genus.

In ptilomerinae the seventh segment has undergone even more drastic modification. In such primitive forms as the subgenus *Proptilomera* of the genus *Ptilomera, Rheumatogonus* and *Potamometropsis* there occur no connexival spines and the posterolateral angle of the seventh segment is simply truncate. The absence of the connexival spines appears to be, therefore, a primitive condition in this subfamily. The posterolateral region of the seventh segment, where connexival spines occur in Gerrinae, has become highly modified in more specialized species of *Ptilomera* and in all other genera except the ones mentioned above. This modification often simulates the connexival spines in Gerrinae but it is not the same, since they occur in more specialized forms in which the seventh segment itself is more or less greatly prolonged. It is of the same secondary nature as that occuring in *Eurygerris cariniventris.* The process of modification of the posterolateral region of the seventh segment, though somewhat difficult to trace due probably to the much smaller numbers of species available for study, will be discussed elsewhere in the proper place for each genus. The ventral apical margin of the seventh segment is provided with a lobate projection in most genera including such primitive forms as *Proptilomera* and *Rheumatogonus*; it does not occur in *Rhyacobates* and *Pleciobates*(?).

In Rhagadotarsinae the seventh segment is simply prolonged and without the connexival spines and the ventral apical margin is simply concave. In Trepobatinae the apical projection of the same nature as that occurring in *Eurygerris cariniventris* occurs in *Trepobates knighti,* and the ventral apical margin is lobately produced in *Metrobatopsis.* In all other species of Trepobatinae the seventh segment is as in Rhagadotarsinae. In Halobatinae the connexival spines are absent, and the ventral apical margin is simply concave in all genera except for *Metrocoris,* in which a lobate development occurs on the ventral apical margin, telescoping the eighth segment above.

The lobate development of the ventral apical margin thus has occurred independently in some of the more specialized genera of

Gerrinae and Ptilomerinae, *Metrocoris* of Halobatinae and in *Metrobatopsis* and *Rheumatometroides* of Trepobatinae. The secondary lateral projections which simulate the connexival spines of the more primitive genera of Gerrinae apparently arose independently in *Eurygerris* of Gerrinae, in many species of Ptilomerinae and in one species of *Trepobates* of Trepobatinae.

The absence of the connexival spines on the seventh segment is a good tribal character in Gerrinae and a subfamily characteristic of Halobatinae, Rhagadotarsinae and Trepobatinae. The progressive median emargination on the ventral apical margin in males of some genera of Gerrinae, and the progressive development and migration of processes on the ventral apical margin in males of some other genera indicate the difference in evolutionary potentialities among these groups. The curious modification in females of the ventral apical margin in *Platygerris, Tachygerris* of Gerrinae, some genera of Ptilomerinae and in *Metrocoris* of Halobatinae provides good generic as well as specific characters. The absence of this modification even in specialized genera of Rhagadotarsinae and Trepobatinae suggests a difference from the other subfamilies in evolutionary potentialities.

The eighth abdominal segment

Since the female genitalia occur partly in this segment the evolution of this segment is discussed separately for each sex.

The male: The most important evolutionary tendency of the eighth segment is, as for the seventh segment, the prolongation of the segment itself. This is true of all groups of Gerridae. In some of the more primitive genera of Gerrinae, such as *Eotrechus, Gigantometra, Limnoporus, Tenagometrella, Charmatometra* and *Eobates,* the eighth segment itself has never become appreciably prolonged. In *Brachymetra, Onychotrechus, Chimarrhometra* and *Amemboa,* in which the seventh segment is not greatly modified in shape, the eighth segment also has never become much modified apart from its prolongation in more specialized species of these genera. A similar condition is also noted in *Eurygerris* and the *Limnometra-Tenagogonus s. str.* complex. In other genera of Gerrinae evolution has proceeded further, to the point where the ventral surface of the segment is more or less greatly modified. In Cylindrostethini the basal ventral region has become more and more depressed and the ventral apical margin has become progressively asymmetrical with the development of a process on one side of the apical margin;

in the most highly specialized genus, *Platygerris,* the eighth segment is most prolonged in *P. caeruleus.* In this species it is, in fact, longer than all the preceding segments together. In *Aquarius* and *Gerris s. str.,* the ventral surface of the eighth segment has become more and more longitudinally elevated at the middle in the more specialized species. In the *Limnogonus s. str.-Limnogonellus* complex the ventral apical margin has become increasingly modified with formation of the processes of various shapes in the middle. In some species of *Tenagogonus s. str.* the ventral surface as well as the ventral apical margin have become curiously modified.

In Ptilomerinae the most primitive eighth segment is seen in *Rheumatogonus,* in which the segment is not even appreciably prolonged in the two species examined; in all other genera the segment has been considerably prolonged. At least in some species of *Ptilomera, Heterobates,* and *Rhyacobates* there occurs a depression on the basal region of the ventral surface, as in *Potamobates* and *Platygerris* of the Gerrinae. In these genera (*Heterobates* and *Rhyacobates*) there also occurs a median longitudinal elevation which is more pronounced apically as in *Aquarius* and *Gerris s. str.* of Gerrinae.

In Rhagadotarsinae the eighth segment is greatly prolonged and longitudinally sulcated in the middle in *Rhagadotarsus,* simply prolonged in *Rheumatobates.* In Trepobatinae the prolongation of the segment occurs in many genera, although in the more primitive species of some genera, like *Telmatometra* and *Trepobates,* the segment is not appreciably prolonged. In some more specialized genera the segment is more or less greatly modified, but neither basal depression nor the median longitudinal elevation on the ventral surface occurs in this subfamily. The direction of evolution is more or less peculiar to each genus; *e. g.,* in *Hynesionella* the ventral surface has become elevated conspicuously laterally; in *Metrobatopsis* it is greatly prolonged and is provided with a wide triangularly depressed area in the apical region of the ventral surface; a similar but lesser development occurs in *Trepobatoides*; in *Halobatopsis* the ventral apical margin is greatly produced as a process in one species. In Halobatinae two pairs of processes, dorsolateral and ventrolateral, become more and more conspicuous through the *Asclepios-Halobates* series. In other genera there exists no such conspicuous modification, and the segment has simply become prolonged in most species.

The ninth abdominal segment

The ninth tergite (suranal plate) in the male: The primitive ninth tergite of the Gerridae was probably rather slender, and the lateral margins more or less parallel to one another as they are in the more primitive existing genera, such as *Eotrechus,* etc. From this probable primitive condition the tergite has undergone various modifications. In Gerrinae the suranal plate is simple or only feebly widened basally in most genera. Rather conspicuous modifications of the lateral margins are seen in *Amemboa.* In this genus the basal lateral processes have become more and more conspicuous in the more specialized species within the genus, and in some of the most specialized species there occurs an additional pair of processes inside the lateral pair of the spinous processes. In *Onychotrechus* and *Chimarrhometra* there occurs no conspicuous modification of the basal lateral margins of the suranal plate. In *Gerrisella* the ninth tergite is provided with a pair of conspicuous processes on the lateral margins. The most conspicuous modification of the suranal plate appears to have occurred in Cylindrostethini, in which the basal lateral margins have become greatly modified progressively with production of the asymmetrical processes on the lateral margins in the smaller, more specialized species of *Cylindrostethus*; and the final stage of modification of the suranal plate attained in the tribe is seen in *Platygerris,* in which the processes are strongly developed only on the right side and are very conspicuous.

In Ptilomerinae the plate is dilated behind its middle. The dilation becomes progressively more conspicuous in *Ptilomera,* from a more generalized, simpler condition in the subgenus *Proptilomera* through a series of species in *Ptilomera s. str.* In Halobatinae the process of modification of the basal to lateral regions of the suranal plate progresses from a relatively generalized condition in *Asclepios* to the highly modified conditions in some species of *Halobates*; while in other genera of Halobatinae no conspicuous modification exists. In Rhagadotarsinae the suranal plate is somewhat dilated but no conspicuous modification occurs. In Trepobatinae conspicuous modifications on the lateral margin exist in *Metrobatopsis, Hynesionella, Rheumatometroides* and *Stenobates.* Such modifications of the lateral margins of the suranal plate occur independently in the more specialized genera of all subfamilies except for Rhagadotarsinae.

Among the related genera, the presence or absence of the processes on the lateral margins constitutes a generic character. The position and shape of the processes also give good taxonomic character at the specific level.

The parameres: The loss of the parameres has occurred independently in some or all genera of all subfamilies except for Ptilomerinae. In Cylindrostethini of Gerrinae the parameres have been virtually lost in the specialized genera, *Potamobates* and *Platygerris,* although they have been retained in *Cylindrostethus.* In Gerrini the parameres are not conspicuous even in the most primitive genus, *Gigantometra.* They are more or less greatly reduced or completely lost in the *Aquarius-Gerris* s. str. complex, in *Limnoporus, Eurygerris,* the *Limnometra-Tenagogonus s. str.* complex, the *Limnogonus s. str.-Limnogonellus* complex, *Tachygerris, Tenagometrella, Tenagometra.* In Eotrechini the parameres are well developed in *Eotrechus,* short but robust in *Onychotrechus,* and completely lost in *Amemboa.* An interesting fact is that the parameres are greatly developed in the otherwise highly specialized genus, *Chimarrhometra.* In the related genus *Amemboa,* however, the basal lateral region of the suranal plate is modified into a conspicuous process but the parameres are absent. The two structures are similar in shape and extend to about the same position, *i. e.,* above the lateral margin of the pygophore. Presumably they replace one another functionally, since when either one is lost or poorly developed the other is well developed. A similar but quite different situation occurs in some species of *Potamobates* and *Platygerris* of Cylindrostethini, in which the suranal plate is asymmetrically modified into a spinous process on one side. This process comes in contact apically with an also asymmetrically produced spinous process from the eighth segment. What function these structures perform we do not know. Since in these genera the paramers have been lost, these structures may have something to do with copulation. In Charmatometrini the paramers are simple but retained in all known species.

In Ptilomerinae the parameres have been retained in all genera. Interestingly, the parameres have apparently undergone modification apically in *Ptilomera* as will be discussed in more detail elsewhere; in the subgenus *Proptilomera* the parameres are simple apically but in *Ptilomera s. str.* the apical portions of the parameres are bent and provided with a dense mass of shaggy hairs. In Halobatinae the parameres are distinctly retained in *Asclepios,* but are reduced and almost unrecognizable in the related, more specialized genus *Halobates.* In all other genera of this subfamily the parameres are retained and are even somewhat conspicuous. In

Rhagadotarsinae the parameres have been lost in both genera. In Trepobatinae the parameres are unrecognizable in *Metrobatopsis* and *Hynesionella* but in these genera there occurs a conspicuous modification on the basal lateral region of the suranal plate, forming a conspicuous process directed ventrad. In all other genera of Trepobatinae the parameres are conspicuous (*Stenobates* was not examined) or reduced but recognizable (*Rheumatometra*).

The evolutionary tendencies of the parameres in the Gerridae can be summarized as follows:

(1) The parameres have had an overall tendency to be lost.

(2) The parameres, when lost or reduced, appear to be replaced functionally by the development of the basal lateral region of the ninth tergite (suranal plate) in more specialized genera. This is true of *Amemboa, Gerrisella, Metrobatopsis,* and *Hynesionella.*

(3) When the reduction of the parameres occurs in relatively primitive genera (Gerrini), the suranal plate is not modified to form the processes on the lateral margins.

(4) With the loss of the parameres both the eighth and ninth tergites are asymmetrically modified (Cylindrostethini).

(5) The parameres have had a tendency to become modified instead of becoming reduced in certain groups.

(*a*) In *Ptilomera,* modification of the parameres has had nothing to do with modification (dilation) of the basal lateral margin of the suranal plate into conspicuous process laterally. Both have evolved independently.

(*b*) In *Chimarrhometra* the parameres have become greatly enlarged, although in a related genus (*Amemboa*) the parameres are lost and the suranal plate is greatly modified.

The shape of the parameres, when present, offers an excellent specific character. The presence or absence of the parameres is constant in most genera.

The Pygophore: Prolongation is one of the most important aspects of evolution of the pygophore, as for the preceding segments, and this has occurred in all subfamilies. In highly specialized genera, such as *Potamobates* and *Platygerris* of the Gerrinae and in some species of *Halobates* of Halobatinae, the pygophore is rotated laterally (to the right). The rotation of the pygophore in these genera is always associated with production of more or less conspicuous asymmetrical processes on the suranal plate and the eighth abdominal segment (*Potamobates and Platygerris* of the Gerrinae), or with production of the asymmetrical processes on the ventral apical margin of the eighth segment (some species of *Halobates*). A peculiar manner of rotation of the pygophore is noted in two species of *Metrobatopsis* of Trepobatinae, in which it is rotated anteriorly, instead of laterally, exposing the ventral side of the pygophore subvertically. Another feature of the evolution of the pygophore is the modification of its ventral surface and apical margin. The apical margin of the pygophore is very conspicuously modified in many species of *Amemboa, Chimarrhometra* (figs. 572, 591, 592, 593) and *Rheumatotrechus* (Kirkaldy, 1908). All these three genera belong to Eotrechini of the Gerrinae, suggesting a peculiar evolutionary potentiality for this particular feature in this tribe. In *Ptilomera* of the Ptilomerinae the progressive prolongation of the pygophore is conspicuous as will be described elsewhere. In other groups there is a trend for the apical margin of the pygophore, though usually not pronounced, to become more or less concave, and in *Eurymetropsis* of the Halobatinae the apical prolongation and bifurcation are very conspicuous. In a species of *Metrocoris* of Halobatinae the apical half is greatly dilated. The occurrence of a median spinous process on the longitudinal axis of the pygophore is a peculiar feature to *Metrobatopsis.*

The degree of rotation of the pygophore as well as the degree of modification of its apical margin varies considerably in various species within the same genus. Therefore, they are generally more important characters at the species-level than at the generic level.

The styloide: The styloide occurs only in *Eotrechus*; in all other species the structure has been lost. Whether the styloide in Heteroptera is homologous with the stylus in lower orders of insects or not is still uncertain. The presence of the styloide probably represents a primitive condition, since the structure tends to be either fused with the pygophore or lost in more specialized groups of the same family (*e. g.,* Aradidae, Usinger and Matsuda 1959).

The endosoma (figures 102-104): In the primitive gerrids the number of well-differentiated sclerotized plates in the apical segment of the endosoma was probably three (dorsal, apical and lateral). This is evidenced by the condition in *Eotrechus,* in which the well sclerotized paired plates number three. Assuming that this is a probable primitive condition in the Gerridae, a general picture of evolution of the sclerotized plates of the endosoma is tentatively suggested in figures 102 to 104.

In hypothetically primitive gerrids each pair (apical, dorsal and lateral) is clearly separated. The next stage in evolution is the acquisition of the small basal plates at the bases of the dorsal plates with the membranous ventral plates bearing the seminal duct (fig. 102). This condition is seen in some more generalized genera of Gerrinae, such as *Gigantometra, Aquarius,* etc. In these forms the definitive dorsal plate extends along the dorsal margin of the endosoma. The paired origin of the resultant plate is clearly indicated by the fact that it is split into two branches at both ends and is more strongly sclerotized on the lateral margins. The apical plate is bifurcate and is located along the apical margin of the endosoma. This plate is separated from the dorsal plate in more primitive genera, such as *Gigantometra, Eotrechus, Aquarius elongatus* and some genera of Trepobatinae; its paired nature is also well indicated by the condition in Eotrechini, in which paired apical plates are loosely connected to each other. The united definitive apical plate is fused with the definitive dorsal plate in the majority of species of Gerridae, so that what appears to be the dorsal plate is strongly turned backward on the apical margin of the endosoma (fig. 103). The basal plates, originally paired and separated from the dorsal plate, have become fused to the dorsal plate. It is important to point out that the absence of the basal plate is almost always accompanied by the absence of ventral plates. The ventral plates are also paired and appear to be primitively membranous as seen in more primitive species of *Aquarius* and *Limnometra.* A final stage of evolution of these plates is shown in figure 104. It has involved fusion and sclerotization of all four plates except the lateral plates, and the elongation of the resultant fused ventral plates. The lateral plates are always paired (sometimes two pairs present), or the plates are ill-defined, these plates having persisted in all genera.

With the above general picture of evolution of the various plates in the endosoma, the following more detailed processes in their evolution in each subfamily become more intelligible.

In Gerrini of the Gerrinae the apical plate is detached from the apex of the dorsal plate in more primitive forms, such as *Gigantometra, Aquarius elongatus,* but the apical plate appears to be fused to the dorsal plate forming an anteriorly directed thick and bifurcate apex of the definitive dorsal plate in most species of *Aquarius, Gerris s. str., Limnometra, Tenagogonus s. str., Limnogonus s. str., Limnogonellus,* and *Tenagometra. Tachygerris* shows an interesting deviation in that the apical plate is clearly detached from the apex of the dorsal plate when it is present, but the tendency is to become lost so that the apex of the dorsal plate reaches only to the middle of endosoma. The basal plate in this tribe is present in all genera. It is detached from the dorsal plate in some species of *Limnogonus*, while in other genera the basal plate is fused to the dorsal plate. The ventral plate is present in all genera of Gerrini. It is bilobed, indicating its paired origin in *Limnometra* and in some species of *Aquarius*, and it is largely membranous; in all others the ventral plates are fused and not bilobed. In the *Limnometra-Tenagogonus s. str.* complex the ventral plate, though always bilobed, tends to be more sclerotized in more specialized species. The lateral plates are always present although hard to recognize in some species, due to sclerotization along the ventral margin of the endosoma.

In Charmatometrini the apical plate is apparently fused to the dorsal plate, while the basal plate is detached from the dorsal plate in *Charmatometra bakeri*, but fused to the dorsal plate in *Brachymetra*. The original paired membranous ventral plates are completely fused and definitively single lobed, and moderately long.

In Eotrechini there is no well-developed sclerotized basal plate in any genus. The seminal duct appears to be borne on the highly membranous process arising directly from the base of the apical segment of the endosoma. This condition was observed in *Onychotrechus sakuntala* in this study. A well-formed ventral plate, supported basally by the well-developed basal plate, thus does not occur in this tribe. The apical plate is always large, rounded, and loosely connected to the apex of the dorsal plate. In *Amemboa* the apical plate is provided with a pair of processes on the ventral side. The lateral plates are always simple and paired, the ventral plate being highly membranous.

Among the genera of Cylindrostethini, the condition of *Cylindrostethus productus* is peculiar in that the only sclerotized plate is the dorsal plate. In another species of *Cylindrostethus* from the Eastern Hemisphere, *C. naiades,* the basal plate is separated from the dorsal plate and bears the membranous ventral plate. In the species of *Cylindrostethus* from the Western Hemisphere the basal plate is indistinguishably fused to the dorsal plate as in *C. naiades* from the Eastern Hemisphere. The lateral plates in the genus always consist of one pair. In *Potamobates* and *Platygerris* the ventral plate is always sclerotized and prolonged among various species. The lateral plates are often represented by two pairs of sclerotized plates.

In Ptilomerinae the definitive dorsal plate never extends beyond the middle of the endosoma except for *Ptilomera* and *Potamometra,* in which it reaches the apical margin of the endosoma. The apical region of the dorsal plate in these two genera is very probably the fused apical plate. In some genera, *e. g., Rheumatogonus, Potamometroides, Rhyacobates* and *Potamometropsis,* the apical plate appears to have been lost and the apical end of the definitive dorsal plate represents the apical end of the veritable dorsal plate. In *Heterobates* the apical plate is connected laterally by a transverse bridge. The line of union of the basal plate to the dorsal plate is recognizable by the difference in degree of pigmentation between the two plates. In *Rheumatogonus* the basal plate is apparently loosely connected to the dorsal plate, and in this respect this genus is more primitive than the others. The originally paired ventral lobes are fused to form a single lobe, membranous at least apically in all genera except *Potamometra,* in which the ventral plate is darkly pigmented and very long. The lateral plates, when present, always consist of a single pair. The general evolutionary trend of the plates in this subfamily is toward the loss of the apical and lateral plates, while in no genus does the ventral plate retain the short bilobed form.

In Halobatinae the apical plate is presumably fused to the dorsal plate in all genera. The basal plate at its base is not fused to the dorsal plate in some species (*Esakia kuiterti, Ventidius werneri, Eurymetra natalensis, Halobates sobrinus*). The ventral plate is single lobed, long, and membranous apically. The lateral plates are sometimes consisting of two pairs (*Eurymetra natalensis*). A slender sclerotized loop embracing the dorsal plate occurs in *Eurymetra natalensis, Ventidius werneri, Esakia kuiterti,* and *Asclepios coreanus.* The major evolutionary trend of the various plates of the endosoma in this subfamily is toward fusion of the plates; loss of plates does not seem to have occurred as far as limited number of species examined indicates. The occurrence of the looped, slender sclerite is peculiar to this subfamily.

In Rhagadotarsinae the major trend is toward fusion of the plates. In both *Rhagadotarsus* and *Rheumatobates* the apical, dorsal, basal, and ventral plates are completely fused, forming a round ring within the endosoma; the lateral plates in this subfamily are small.

In Trepobatinae the major evolutionary trend involves the loss of the basal and ventral plates. One may question whether the absence of these plates arose directly from the condition found in *Eotrechus* of the Gerrinae or is a secondary loss. The evidence is in favor of the latter alternative. First, in the related but generally more primitive subfamily Rhagadotarsinae, both plates, though completely fused, obviously exist; second, in relatively primitive genera of this subfamily (*Trepobates, Cryptobates, Trepobatoides*) as well as in a more specialized genus (*Hynesionella*) the basal and ventral plates are present. The apical plate is always present. It is not fused to the dorsal plate in *Metrobates* and *Halobatopsis* and is fused only by a narrow bridge to the dorsal plate in *Telmatometra;* in all other genera the apical plate is completely fused to the dorsal plate. The lateral plates are long and paired; sometimes they are hardly recognizable due to sclerotization of the endosoma.

Prolongation of the apical segment of the endosoma: Prolongation of the apical segment of the endosoma occurs in Gerrinae; in other subfamilies the prolongation is not pronounced. Apically the endosoma is not at all elongated in the primitive genus *Gigantometra* of the Gerrini. In *Aquarius* it is not prolonged in primitive species, such as *G.* (*A.*) *elongatus,* but lengthens progressively in a series of more specialized species as is shown in figures 212 to 216. The prolongation of the endosoma is also conspicuous in the *Limnogonus s. str.-Limnogonellus* complex and in *Eurygerris.* In Charmatometrini and Eotrechini there occurs no conspicuous lengthening of the endosoma. In Cylindrostethini the apical segment of the endosoma is prolonged in more specialized genera, such as *Potamobates* and *Platygerris,* but the prolongation in these genera appears to be of different nature from that occuring in Gerrini in that the endosoma as a whole has been prolonged instead of merely its apical region.

Undoubtedly, the differences in shape of the various plates and presence or absence of certain plates provide excellent specific characters as in other families of Heteroptera. Although the number of species investigated in this study is limited for each genus and often the generic differences are not well marked, it is clear from the foregoing discussion that the general arrangement of the various plates and the evolutionary tendencies noted are more or less peculiar to each subfamily or tribe, and appear to be of taxonomic importance at the subfamilial and tribal levels. Certain peculiar features, *e. g.,* the tendency to lose the apical plate in *Tachygerris* seem to be characters of generic importance.

The female genitalia

A well-developed ovipositor, according to Reuter (1910), is primitive in Heteroptera. In the Gerridae the well-formed long ovipositor is present only in Rhagadotarsinae, in which it serves presumably for the insertion of the egg into the tissues of plants (Hungerford, 1954). Whether this peculiar development of the ovipositer in this subfamily of the Gerridae is a primary or secondary condition is not certain. In this subfamily the first and second valvulae are greatly prolonged in both genera, but the basic structural plan is the same as in other subfamilies of the Gerridae; the rami of the first and second valvulae are connected to the black subtriangular plate at the apex of the process of the ninth tergite; the second valvifer as well as the third valvulae have been lost as in other subfamilies. In all other subfamilies of the Gerridae the first and second valvulae are less developed than in Rhagadotarsinae. The first valvulae either are not differentiated into the outer and inner lobes or are so differentiated only apically, if at all, in Ptilomerinae. In Gerrinae, Halobatinae, and Trepobatinae they are well differentiated into outer and inner lobes and the latter are usually attached to the vulva; the inner lobe is further split into two slender apical processes in many genera of Trepobatinae, and this is probably a specialized condition. The ramus is attached to a black elongate sclerite above the apex of the process from the ninth tergite in Rhagadotarsinae. This sclerite has apparently reduced to assume a crescent shape in at least some genera of all the other subfamilies, and has been completely lost in many genera. The ramus of the first valvulae has shifted its point of attachment to the outer margin of the usually membranous process arising from the ninth tergite. The ramus of the first valvula is indistinguishably fused to the process in many genera but is often recognizable by different degrees of pigmentation in Ptilomerinae and Trepobatinae.

The second valvulae are pointed apically, forming a complete sheath above the first valvulae in Rhagadotarsinae. In all other subfamilies the valvulae are apically free from each other, connected by the intervalvular membrane. The apex of each valvula usually extends beyond the apical margin of the intervalvular membrane. The ramus is always slender, apparently shifted its position to the inner margin of the thicker ramus of the first valvula accompanied by the loss of the second valvifer. The vestigial third valvulae are retained only in Charmatometrini of Gerrinae. The apical margin of the intervalvular membrane is highly sclerotized in Cylindrostethini, although it is membranous or thinly sclerotized in the other tribes of Gerrini and other subfamilies of Gerridae.

In spite of a limited number of species studied it seems clear that the female genitalia offer excellent taxonomic characters at the subfamilial or tribal level.

The forewing

The most complete, hence the most primitive forewing venation is found in *Ptilomera, Rheumatogonus,* and *Rhyacobates* of Ptilomerinae (figs. 612, 740), in which Sc is well retained without forming the embolium along the costal margin of the wing. Veins R + M and Cu arise independently from very near the base of the wing; R + M joins Sc at the apical one fifth of the wing; Cu is joined with R + M before the middle of the wing by a cross vein. A joins with Cu in their apical thirds. In *Potamometra* (fig. 645) of the same subfamily, R + M and Cu are completely fused basally, R + M + Cu branches into upper R + M and lower Cu at the basal one third of the wing, R + M further diverges into R and M respectively, and each is connected with Sc and Cu apically.

While Sc_2 arises always from near the middle of the costal margin of the wing, the point of separation of the basal R + M into R and M shifts more and more distally in specialized genera of Gerrinae, and this shift of point of separation has evidently occurred independently in three different tribes, *i. e.*, Gerrini, Eotrechini, and Cylindrostethini.

In Gerrini the point of separation of R and M in the most primitive genera (*Gigantometra, Aquarius, Gerris s. str., Limnoporus, Limnometra, Tenagogonus s. str.*, most species of *Limnogonus s. str.*, and *Limnogonellus* and one specialized genus *Gerrisella*) is near the middle of the hemelytron, a point more distal to the point of separation in *Potamometra* of Ptilomerinae, while the point of separation of R and M is more caudal in one specialized genus (*Eurygerris*) and in *Tachygerris,* which deviates in some other characters. In Cylindrostethini the point of separation of R and M is near the middle of the hemelytron as in most genera of Gerrini (fig. 428), but in the specialized genera, *Potamobates* and *Platygerris,* the point of separation of R and M from the basal R + M is much more distal (figs. 463, 484). In Eotrechini the point of separation of R and M is near the middle in two more primitive genera, *Eotrechus* and *Onychotrechus,* but the point of separation is definitely much more distal in a more specialized genus, *Amemboa* (fig. 584), than in the two other genera.

Because of this trend the vein Sc_2 becomes united with R + M at the point anterior to the point of separation into R and M in the above mentioned specialized genera. In Charmatometrini, however, the point of separation of R and M is near the middle of the hemelytron and Sc_2 is joined very near or at the point of separation of R and M in all three genera, as in the primitive genera in the other three tribes. The process of evolution of the veins discussed above is thus beautifully traceable from the most primitive condition in the three genera of Ptilomerinae to the most specialized condition in some specialized genera in Gerrinae, and the mechanism involved is simply the greater degree of fusion of R, M, and Cu veins.

In Halobatinae the wing venation is further reduced and the fusion is more advanced. The embolium is always formed along the costal margin of the hemelytron. In *Metrocoris* (fig. 779) R + M + Cu is distinct and branches into R + M and Cu; R + M is connected with the embolium by two oblique veins; Cu is connected with A at the apical third of the hemelytron. In *Ventidius* (fig. 821) the basal region of R + M + Cu is obliterated and the proximal oblique vein connecting the embolium and R + M is lost. In *Esakia* (fig. 855) the venation is further simplified. Vein R + M + Cu branches into two long simple veins anterior to the middle of the wing, the upper branch going along the costal margin of the wing nearly to the apex and lower vein also, after being joined by A at the middle, extends to the apical margin of the wing. Among Rhagadotarsinae, the venation is similar to that of typical Gerrinae in the genus *Rhagadotarsus* (fig. 886) except that R + M does not branch into R and M apically, a condition more specialized for these veins than in some most specialized genera of Gerrinae; oblique Sc_2, the obscure short vein connecting the rear margin of the hemelytron at the middle with A, and Cu are all present. In *Rheumatobates* the venation is further reduced. The vein A does not continue beyond the middle of the wing and is not joined to Cu. An important feature is a line of weakness which is indicated by a slightly pigmented or white transverse line extending to the middle from the apical margin of the hemelytron in both genera of this subfamily. This line of weakness is limited basally by the vertical line of weakness at a little behind the middle of the wing in *Rheumatobates.* In Trepobatinae the basal region of the hemelytron is strongly coriaceous, with a well-developed embolium which never extends beyond the basal coriaceous region. The basal coriaceous region occupies only the basal third of the hemelytron in some genera (*Metrobatopsis, Naboandelus*); R + M + Cu divides into two branches, R + M and Cu. The former is joined to the broad embolium at its apical corner and is continuous nearly to the apex of the hemelytron. The latter joins A beyond the middle of the hemelytron, then extends apically in most genera. The transverse line of weakness occurs in all genera as in Rhagadotarsinae, suggesting a common ancestry.

Because of its stability, the wing venation in Gerrinae offers excellent subfamily characters. In some genera of Gerrinae, Sc_2 is often joined with $R + M$ before the point of separation into R and M; this varies within genera and is even subject to individual variation in some species, so that this feature may be neither a generic nor a species character. Both in very primitive and highly specialized genera the location at which Sc_2 joins to $R + M$ or R is highly constant and can be of taxonomic importance at the generic level. In Ptilomerinae the venation seems to be a little more variable than in Gerrinae at the generic level. In Halobatinae the venation seems to be of taxonomic importance at the generic level. In Rhagadotarsinae the venation is evidently an important taxonomic character at the generic level. The coriaceous basal region and the broad embolium are characteristics of the subfamily Trepobatinae. As far as the venation is concerned there appears to be very little difference among genera of this subfamily. The occurrence of the transverse line of weakness in the hemelytron in Rhagadotarsinae and Trepobatinae is correlated with the nature of the definitive intersegmental suture between the mesonotum and metanotum occurring only in these two subfamilies.

II. EVOLUTION OF THE LEGS AND ANTENNA

1. Postembryonic development

During the study of structural evolution it became increasingly apparent that the proportional lengths of leg and antennal segments have been altered with change in body size in evolution. This was suspected to be a case of allometry. The next step taken, therefore, was to study the postembryonic development of representative species of each major group to see whether proportional lengths of antennal and leg segments vary ontogenetically in the same manner as they appear to vary phylogenetically among adults of different sizes.

The materials available for study were *Metrocoris histrio* (Buchanan-White) (Halobatinae) which was kindly sent to me by Professor S. Miyamoto, Japan; *Gerris (Aquarius) remigis* Say, *Gerris (Gerris) marginatus* Say (Gerrinae), *Trepobates knighti* Drake and Harris (Trepobatinae), all collected at Lone Star Lake, near Lawrence, Kansas, and *Rheumatobates rileyi palosi* Blatchley collected at a pond on the campus of The University of Kansas by the author. The number of individuals of each stage was sometimes insufficient, but at least a few individuals of each stage were available for study, as noted from table 1.

It was observed that the lengths of antennal and leg segments were more constant than the body size among individuals at each stage. The lengths of the segments are, therefore, more reliable criteria in deciding stages of development than the body size. The inconstancy of the body size at each developmental stage may possibly be due to the fact that different sexes are contained in the materials. In *Rheumatobates rileyi palosi* *, for which only the female individuals were measured, the body size and the segmental lengths appeared to be more highly correlated than in the other species. Clerk and Hersh (1939) found recognizable sexual and individual differences in relative growth ratios of appendages to the body size in *Notonecta.* It should be added that the five individuals of the first stage nymph of *Gerris (Aquarius) remigis* studied may, by sampling error, be represented by relatively large individuals only.

Relative growth: In 1924 J. Huxley put forward an exponential formula which expresses, by means of abstract values, the rate of growth of any one allometrically growing organ (Y) in relation to the total body size or to another organ whose growth is taken as standard (X). The formula is thus $Y = bX^k$ where b is the initial growth index, or the value of Y when X equals unity, and k is the equilibrium constant by which Y grows in relation to X throughout the ontogenetic stages. This constant is also called the growth ratio and this term is used in the following discussion.†

The assumption, implicit in the application of the formula to data, is that differences in size correspond to differences in developmental stage. Hemimetabolous insects such as the gerrids are extremely favorable for the study of relative growth, since in these insects comparable stages (instars) are well marked off and the structures do not undergo drastic modification until the adult stage is reached. Taking the total length of the body as the standard X, and using the lengths of the front, middle, and hind leg segments, as well as antennal segments for the differentially growing parts Y at each developmental stage, the data were fitted to the formula $Y = bX^k$ (From this formula is derived: $\log Y = \log b + k \log X$; this

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* Sexual dimorphism is evident even at the first stage in this species.

† Since the correlation coefficients between the length of body and segments are over 0.99 in the great majority of cases in this study, Imbrie's (1956) bivariate statistical technique is not used.

TABLE 1.—Mean values of the body length, antennal and leg segments.
Gerris (Aquarius) remigis Say

Stage	No. of individuals	Length of body	Antennal segments				Front leg			Middle leg			Hind leg		
			1	2	3	4	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.
1	5	39.3 (38–42.5)	5.0	2.7	3.6	9.5	8.9	9.0	3.7	18.7	19.6	15.9	17.8	10.1	8.7
2	10	54.1 (49–59)	6.8	4.0	5.6	10.5	13.1	12.9	5.3	33.4	35.3	25.4	31.5	20.0	12.6
3	10	76.2 (70–80.2)	11.4	6.6	8.3	13.1	21.6	20.0	7.8	56.5	53.3	33.8	52.8	31.7	17.4
4	10	113.1 (96–132)	19.0	9.8	11.4	16.6	34.7	31.1	10.7	90.1	80.1	46.9	83.7	55.0	24.8
5 ♂	10	173.6 (145–195)	30.2	15.9	17.2	20.5	55.2	50.0	18.6	139.8	120.1	64.8	130.2	97.8	37.2
5 ♀	10	169.9 (145–190)	29.8	14.9	16.2	20.1	51.6	47.7	18.3	133.4	115.1	63.5	124.4	93.0	35.7
Adult ♂	5	244.6 (240–257)	41.3	20.2	19.9	22.7	77.8	68.2	25.4	179.8	153.8	80.1	173.0	142.2	47.8
Adult ♀	10	256.4 (251–265)	41.6	20.0	19.8	21.9	73.8	65.6	23.4	172.2	151.3	78.2	161.8	131.7	45.3

TABLE 1.—Mean values of the body length, antennal and leg segments.—*Continued*

Gerris (Gerris) marginatus Say

Stage	No. of individuals	Length of body	Antennal segments				Front leg			Middle leg			Hind leg		
			1	2	3	4	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.
1	5	20.58 (20–21.4)	3.0	1.7	2.0	7.5	6.0	6.0	3.0	10.7	13.0	11.8	10.3	6.7	6.7
2	10	30.95 (27–36)	4.8	2.9	3.4	9.7	9.0	8.8	3.2	18.8	19.1	15.7	17.7	10.2	9.0
3	10	50.6 (44–57)	7.7	4.5	4.9	12.2	12.9	12.6	4.7	30.1	27.9	21.4	28.0	14.5	10.9
4	10	72.8 (66–86)	11.0	6.4	7.1	15.5	20.2	18.8	6.4	48.3	41.3	31.7	44.7	22.9	16.2
5 ♂	6	110.67 (102–118)	16.6	9.6	9.7	18.3	27.8	26.1	9.5	68.8	55.6	42.8	67.3	35.2	78.0
5 ♀	3	106.7 (102–115)	17.5	9.5	9.6	18.5	29.3	27.6	9.7	72.0	60.7	44.7	71.2	37.2	23.0
Adult ♂	10	157.4 (152–163)	20.2	10.7	10.6	18.3	36.4	32.4	9.5	88.3	69.7	49.7	87.8	47.3	25.1
Adult ♀	2	177.5 (174–181)	22.0	11.8	11.3	18.5	37.5	34.5	11.5	95.0	79.0	56.7	95.0	57.0	29.0

TABLE 1.—Mean values of the body length, antennal and leg segments.—*Continued*

Metrocoris histrio (B. = White)

Stage	No. of individuals	Length of body	Antennal segments				Front leg			Middle leg			Hind leg		
			1	2	3	4	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.
1	5	50.6 (48.5–52)	5.2	4.6	6.8	9.1	12.8	11.5	7.3	30.4	30.0	38.8	30.1	16.9	11.0
2	6	68.5 (54.0-70.5)	9.7	6.9	9.7	10.7	20.0	17.2	9.7	50.1	42.0	47.5	49.3	24.6	14.5
3	5	84.6 (73–91.0)	16.2	9.5	12.0	12.0	30.3	25.2	11.2	79.2	61.2	56.3	80.1	39.0	18.7
4	5	116.0 (105–127)	29.1	14.1	18.0	17.0	45.5	38.4	16.8	119.1	89.0	63.9	119.7	64.8	22.4
5 ♂	4	145.0 (143–148)	58.6	26.4	27.0	21.6	71.0	61.3	26.8	184.0	139.8	83.7	190.3	117.3	27.3
5 ♀	4	142.0 (129–152)	48.3	22.0	25.8	21.1	67.5	57.1	23.4	170.0	133.0	77.6	177.5	108.0	27.2
Adult ♂	7	191 (178–212)	91.3	38.0	34.2	25.0	94.0	82.1	34.8	239.3	194.0	88.1	250.3	162.0	29.9
Adult ♀	5	177.6 (168–191)	65.6	30.2	51.2	23.0	83.0	92.2	29.7	207.0	163.6	79.6	213.6	139.0	26.3

TABLE 1.—Mean values of the body length, antennal and leg segments.—*Continued*

Rhematobates rileyi palosi Blatchley

Stage	No. of individuals	Length of body	Antennal segments				Front leg			Middle leg			Hind leg		
			1	2	3	4	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.
1 ♀	2	30.0 (30–30)	…	…	…	…	…	…	…	15.0	12.8	12.0	8.5	8.3	6.8
2 ♀	7	38.5 (37–41)	…	…	…	…	…	…	…	20.7	17.2	15.2	10.5	10.0	8.3
3 ♀	10	49.0 (45–51)	…	…	…	…	…	…	…	29.1	22.5	19.8	15.0	12.6	10.0
4 ♀	8	64.5 (62–67)	…	…	…	…	…	…	…	40.2	31.4	26.5	21.7	17.8	12.7
5 ♀	9	91.4 (90–93)	…	…	…	…	…	…	…	55.5	45.0	36.9	31.8	24.0	17.7
Adult ♀	5	109.0 (106–111)	…	…	…	…	…	…	…	69.0	60.5	45.1	42.0	31.2	19.7

TABLE 1.—Mean values of the body length, antennal and leg segments.—*Concluded*

Trepobates knighti Drake

Stage	No. of individuals	Length of body	Antennal segments				Front leg			Middle leg			Hind leg		
			1	2	3	4	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.	Fem.	Tib.	Tars.
1	10	35.4 (30.6–40.0)	4.3	2.8	3.1	6.7	7.2	6.8	4.4	14.3	22.8	17.5	14.0	11.2	9.1
2	10	48.2 (42.0–51.5)	6.0	3.7	3.9	8.1	10.6	9.7	5.5	19.2	31.6	22.3	20.2	14.1	10.9
3	10	65.0 (60.0–70.0)	8.9	5.3	6.2	10.5	15.4	12.6	7.8	28.0	45.8	31.2	30.7	19.5	14.6
4	10	85.9 (77.0–93.0)	13.0	8.1	8.9	13.2	22.4	18.5	10.3	38.0	63.9	42.5	45.0	26.0	19.3
5 ♂	8	113.38 (101–119)	21.3	12.1	13.9	18.1	36.0	28.0	15.1	52.1	92.8	59.1	68.0	34.2	25.6
5 ♀	6	123.2 (115–128)	20.6	12.2	13.4	18.9	32.2	27.0	16.2	56.0	98.5	62.5	70.5	37.3	27.0
Adult ♂	10	129.7 (125–132)	36.2	19.1	20.0	20.7	53.3	38.1	19.8	67.5	126.3	72.2	97.1	45.0	30.5
Adult ♀	5	146.6 (142–150)	29.9	17.7	19.8	21.0	47.6	34.4	21.0	72.8	133.6	84.4	99.2	48.0	33.6

TABLE 2.—The values of the constants of the relative growth function.

Gerris (Aquarius) remigis Say

	k	S^2	b	S^2
1st antennal segment	1.2166	0.0060	−1.2487	0.0026
2nd antennal segment	1.1382	0.0025	−1.3661	0.0010
3rd antennal segment	0.9423	0.0045	−0.8875	0.0020
4th antennal segment	0.5329	0.0019	0.1100	0.0008
Front femur	1.2032	0.0010	−0.9614	0.0005
Front tibia	1.1256	0.0012	−0.8307	0.0004
Front tarsus	1.0417	0.0069	−1.0810	0.0003
Middle femur	1.2258	0.0019	−0.5980	0.0086
Middle tibia	1.0673	0.0016	−0.3120	0.0069
Middle tarsus	0.8260	0.0052	−0.0420	0.0023
Hind femur	1.2191	0.0067	−0.1149	0.0030
Hind tibia	1.3997	0.0049	−0.7914	0.0022
Hind tarsus	0.9247	0.0042	−0.5064	0.0019

Gerris (Gerris) marginatus Say

	k	S^2	b	S^2
1st antennal segment	0.9219	0.0018	−0.6928	0.0007
2nd antennal segment	0.8855	0.0016	−0.8703	0.0006
3rd antennal segment	0.7914	0.0052	−0.6643	0.0020
4th antennal segment	0.4294	0.0034	0.3523	0.0013
Front femur	0.8764	0.0059	−0.3560	0.0023
Front tibia	0.8299	0.0042	−0.2979	0.0016
Front tarsus	0.6509	0.0042	−0.4230	0.0016
Middle femur	1.0164	0.0032	−0.2518	0.0012
Middle tibia	0.8223	0.0009	0.0569	0.0004
Middle tarsus	0.7060	0.0027	0.1574	0.0010
Hind femur	1.0350	0.0028	−0.3030	0.0011
Hind tibia	0.9620	0.0017	−0.4399	0.0006
Hind tarsus	0.6620	0.0020	−0.0447	0.0008

Metrocoris histrio (Buchanan-White)

	k	S^2	b	S^2
1st antennal segment	2.1900	0.0032	−3.0220	0.0014
2nd antennal segment	1.6240	0.0083	−2.1390	0.0035
3rd antennal segment	1.2490	0.0029	−1.3519	0.0012
4th antennal segment	0.7840	0.0032	−0.3850	0.0014
Front femur	1.5196	0.0056	−1.4726	0.0024
Front tibia	1.5050	0.0027	−1.5076	0.0011
Front tarsus	1.2010	0.0069	−1.1470	0.0029
Middle femur	1.5596	0.0195	−1.2020	0.0054
Middle tibia	1.4210	0.0157	−0.9600	0.0067
Middle tarsus	0.6270	0.0171	0.5260	0.0072
Hind femur	1.6170	0.0073	−1.3026	0.0031
Hind tibia	1.7820	0.0035	−1.8426	0.0015
Hind tarsus	0.7340	0.0064	−0.1805	0.0027

TABLE 2.—The values of the constants of the relative growth function.—*Concluded.*

Trepobates knighti Drake and Harris

	k	S^2	b	S^2
1st antennal segment	1.5780	0.0199	-1.8832	0.0076
2nd antennal segment	1.4525	0.0139	-1.8590	0.0053
3rd antennal segment	1.4321	0.0075	-1.7760	0.0029
4th antennal segment	0.8196	0.0057	-0.4590	0.0022
Front femur	1.4985	0.0066	-1.4980	0.0025
Front tibia	1.3032	0.0052	-1.2150	0.0020
Front tarsus	1.1590	0.0038	-1.1906	0.0012
Middle femur	1.1780	0.0014	-0.6822	0.0005
Middle tibia	1.2970	0.0012	-0.6665	0.0005
Middle tarsus	1.0863	0.0056	-0.4325	0.0021
Hind femur	1.4707	0.0017	-1.1575	0.0007
Hind tibia	1.0523	0.0043	-0.6150	0.0016
Hind tarsus	0.9611	0.0007	-0.5600	0.0003
Rheumatobates rileyi palosi Blatchley				
Middle femur	1.1396	0.0022	-0.4820	0.0004
Middle tibia	1.1560	0.0008	-0.5960	0.0002
Middle tarsus	1.0160	0.0014	-0.4200	0.0003
Hind femur	1.2587	0.0014	-0.6620	0.0003
Hind tibia	1.0440	0.0006	-0.6510	0.0001
Hind tarsus	0.8633	0.0007	-0.5600	0.0003

means that if the logarithms of the sizes are plotted we should expect a straight line, from the slope of which the value of k can also be determined). The values b and k thus obtained are shown in the table 2 (all the data are weighted by the sample sizes at each developmental stage).

In figure 108 four antennal segments (Y) and the length of body (X) in *Metrocoris histrio* are logarithmically plotted. It is noted that they conform approximately to the law of simple allometry. Note the nearly straight line as far as the fifth nymphal stage, with a decline in slope at the final stage of development for all four segments. Note also that the broken lines, which indicate the development of the segments in the female, decline more from the fourth developmental stage on. Similar conditions are also noted for all other leg and antennal segments in all species studied, as will be immediately noted from the figures 109, 110, etc.

Simple allometry in the strict sense, *i. e.*, exactly the same growth ratio throughout developmental stages for each segment, apparently does not exist. Differences in growth ratio at different stages sometimes appear to be considerable. It is, however, an overall growth slope throughout the postembryonic developmental stages for each segment as expressed by the regression line and the regression coefficient (the value of k in terms of the allometric equation) that are the primary concern here, so that the growth pattern for each segment at each developmental stage is not analyzed.

It should be pointed out, however, that there is either increase or decrease in growth ratio at the final stage of development for almost all segments in all species studied. The increase occurs consistently in *Trepobates knighti* (fig. 110, etc.) and *Rheumatobates rileyi palosi* (fig. 141, etc.), and the decrease occurs consistently in the two species of *Gerris* studied and in *Metrocoris histrio* (fig. 108, etc.). The data as well as figures consistently indicate that the growth ratio is greater for the males than for the females during the later stages of development for all segments.

Among other aquatic Hemiptera, Clark and Hersh (1939) have shown the existence of approximately single phase allometry in *Notonecta*. Sprague's (1956) study on the postembryonic development of structures in *Hydrometra martini* also indicates the presence of a roughly single phase allometric growth for various structures including legs, although she did not discuss it fully in terms of allometry.

The comparison of growth ratios: The comparison of the relative growth ratios among different segments is shown in table 3. In the table the signs $>$ or $<$ indicate the relation in which the growth ratios between the two comparable segments are significantly different ($P<0.05$ or higher); $\geqq$ or $\leqq$ indicate the relation in which the relative growth ratios between the two segments are different at the level of $0.1>P>0.05$; $=$ indicates the relation where the growth ratios of the two segments are different at the level of $P>0.1$.

Since the number of individuals measured at each developmental stage is different at different stages and different species, the mean values of body and segmental lengths are used in calculating growth ratios and initial growth indices. Therefore, $N = 6$ in using the above formulae. If the measurements for all individuals (*e. g.*, when the numbers of individuals at different stages are the same), instead of mean values at each stage, were calculated the value of N increases, and the value of S^2 decreases accordingly. It should

TABLE 3.—Comparison of growth ratio among segments.*

	G. remigis	*G. marginatus*	*M. histrio*	*T. knighti*	*R. rileyi palosi*
Antenna	1=2>3>4	1=2=3>4	1>2>3>4	1=2=3>4	
Front leg.....	Fem.≧Tib.=Tars.	Fem.=Tib.≧Tars.	Fem.=Tib.>Tars.	Fem.≧Tib.=Tars.	
Middle leg....	Fem.>Tib.>Tars.	Fem.≧Tib.≧Tars.	Fem.=Tib.>Tars.	Fem.<Tib.>Tars.	Fem.=Tib.>Tars.
Hind leg.....	Fem.=Tib.>Tars.	Fem.=Tib.>Tars.	Fem.=Tib.>Tars.	Fem.>Tib.=Tars.	Fem.>Tib.>Tars.

* To see the difference in initial growth indices and growth ratios t-test were used, The formulae are:

$$S^2_K = \frac{\Sigma d^2 y.x}{(N-2)\Sigma x^2}$$

$$t = \frac{K_1 - K_2}{\sqrt{S^2_{K_1} + S^2_{K_2}}} \qquad t = \frac{b_1 - b_2}{\sqrt{S^2_{b_1} + S^2_{b_2}}}, \text{ where } \quad S_b = Sy.x \sqrt{\frac{1}{N} + \frac{\bar{x}^2}{\Sigma x^2}}$$

$$Sy.x = \sqrt{\frac{\Sigma d^2 yx}{N-2}}$$

therefore be borne in mind in reading the following discussion that the significance levels would be higher than those indicated in the table 3, if the latter method were used in calculation.

Different micrometer units were used for measurements of leg and antennal segments in *Trepobates knighti, Rheumatobates rileyi palosi* and *Metrocoris histrio* from those used for the same in the two species of *Gerris*, so the b values between the two groups are not comparable.

2. Evolution of the leg and antennal segments in adult phylogeny

Westoll (1950) classified several different types of relative growth as follows:

(*a*) ontogenetic relative growth (heterauxesis), and

(*b*) absolute size allometry (allomorphosis) of essentially adult material, of several kinds, *e. g.*,

(*i*) members of different contemporaneous stocks or races of species (race allomorphosis)

(*ii*) members of different species of the same genus, without paying attention to difference (usually small) in geological age (species-form allomorphosis, and similarly genera-form allomorphosis, etc.)

(*iii*) members of a lineage, showing progressive change in size, and of known relative geological age (lineage allomorphosis).

The problem here investigated, as already noted, is primarily to see how the ontogenetic relative growth (heterauxesis) relates to adult phylogeny, or species-form allomorphosis and genera-form allomorphosis in the above classification by Westoll. If different species of the same genus have essentially similar allometric growth patterns, *e. g.*, for the leg and antennal segments, the points representing the lengths of segments in adults would be expected to be on or close to the growth lines for the corresponding segments in a representative species for which ontogenetic data are available. The locations of points on or along the growth lines would depend on different body sizes reached by different species. The regression lines for different segments of more than one species (often many) of adults would be on or closely parallel to the growth lines for the corresponding segments. The line based on more than one species of adults is here called the allomorphic line, and the allomorphic slope refers to the slope of such a line in distinction from the growth line and growth slope respectively. While the regression lines for many congeneric adult species (allomorphic lines) more or less conform to the growth lines in direction, they sometimes deviate greatly from the growth lines due to specific differences in the allometric growth mechanisms. Allomorphic lines and slopes of this nature are called the secondary allomorphic lines and slopes (fig. 147, B. to F., indicated by a) in distinction from the former type of allomorphic lines and slopes.

The allomorphic line expressed by the regression line also does not always indicate the underlying growth pattern or the secondary allomorphic trend, since the points for the segments tend to aggregate within a certain area when the range of body size is small. It does indicate the underlying growth pattern or the secondary allomorphic trend only when the range of body size among species is sufficiently great and the body sizes are distributed more or less evenly. The allomorphic trend seen in the relations between the segments and the body size in the species with extreme body sizes within a given group of species has, therefore, often more biological meaning than the allomorphic line based on the regression line.

In the following discussion often incomplete data based on the highly limited numbers of museum specimens, and the literature treating the postembryonic development of the body size, legs and antennae (also based on more or less highly limited numbers of individuals, and the number of individuals measured often not recorded) are referred to. These data are, by their very nature, not highly reliable. They were, however, used to see over-all growth patterns for the structures concerned, and they often gave clues in interpreting what has probably happened to these structures in evolution of various groups of the Gerridae. After the completion of this work I had a chance to collect the nymphs and adults of sixteen species representing eight genera of the Gerridae in Costa Rica and Panama. They are now under study and the data cannot be fully included in this work. The preliminary data obtained from the study of these species, however, are occasionally referred to in the following discussion. In any case the interpretations or suggestions based on the incomplete data need to be verified in the future.

The length of antennal and leg segments of adults are based on one individual of each species taken at random from the museum specimens. They are shown in table 16. For many species only a single specimen or highly limited number of specimens were available.

The antennae

Gerrini: In fig. 111 are shown the postembryonic growths of the first and fourth antennal segments in the two species of *Gerris* studied, together with data for the same two segments in adults of the other species of *Gerris* (smaller points for different nymphal stages). The round black spots representing the first antennal segments in the various species of the subgenus *Aquarius* conform fairly well in slope to the growth line for the same segment in G. *(A.) remigis.* Most of the triangular points representing the various species of the subgenus *Gerris s. str.* also conform fairly well to the growth line for the first segment in G. *(G.) marginatus.* The allomorphic lines for both subgenera rather clearly reflect a difference in growth ratio for the first segment between the two subgenera (1.2166 and 0.9219 in G. *(A.) remigis* and G. *(G.) marginatus* respectively, different at the level of $P<0.05$).

There is no statistically significant difference in growth ratios for the fourth segment in the two species studied. This suggests that there would be no significant difference in the allomorphic slope for this segment if similar growth ratios have been inherited in the species of both subgenera. The points representing the fourth segments in adults of both subgenera continually fall below and along the growth line for this segment in the two species of *Gerris,* indicating that the growth ratio for the fourth segment is presumably much the same in all species belonging to two subgenera. The fourth segment in G. *(G.) marginatus* practically does not grow at the final stage of development and the same may probably be true of other species, judging from the positions of the points which come considerably below the growth line for the same segment in *G. (G.) marginatus.*

Since the growth ratios for the first segments are much greater than those for the fourth, and the growth ratios for the fourth segments are much the same in the two species belonging to different subgenera, the first segment is relatively longer than the fourth in the larger species *(Aquarius)* and relatively shorter in the smaller species *(Gerris s. str.).* Similarly, since growth ratio for the second segment is considerably greater than that for the third segment in *Gerris (Aquarius) remigis* ($0.05 > P. > 0.002$), it is expected that the second segment is relatively longer in the larger species than in the smaller species, assuming that similar growth patterns for these two segments have been inherited by the other species of *Aquarius.* This assumption appears to be true. It is noticed from table 16 that in a majority of species of *Aquarius* the second segment is distinctly longer than the third, and the second segment is longest (in relation to the third) in the largest species, *G. (A.) elongatus* Uhler. In contrast, there is no statistically significant difference in growth ratios between the second and third segments in *G. (Gerris) marginatus,* and the second segment is about as long as the third in a majority of species of the subgenus *Gerris.*

All the above facts strongly indicate that the species belonging to each subgenus share essentially a similar growth ratio for each segment.

In the subgenus *Limnoporus* of the genus *Gerris* (fig. 111) the points for the first segments fall roughly on the allomorphic line for *Aquarius,* although those for the fourth segments (signs X_4) fall much above the allomorphic line for the same segment in *Aquarius* and *Gerris s. str.* The second and third segments in *Limnoporus* are considerably longer than those in *Aquarius* and *Gerris s. str.* of equivalent body lengths. In the three larger species of *Limnoporus* the second segment is distinctly longer than the third, but in the smaller species, *G. (L.) canaliculatus,* the segments are equal in length, suggesting the presence of a greater growth ratio for the second than for the third in this subgenus, as in *Aquarius.*

In *Eurygerris* each species has apparently quite different growth patterns for the antennal segments as far as the preliminary data under study indicate. The lengths of second and third segments in *Eurygerris* are longer than those in *Gerris* of equivalent body lengths. In *Gerriselloides* all four segments are about equal in lengths to those in the species of *Gerris s. str.* of corresponding body sizes, suggesting that the growth ratios for all segments are presumably much the same as in *Gerris s. str.* In *Gerrisella* the fourth segment is much shorter than the fourth segment in *Gerris s. str.* although in *Gerrisella,* which is represented by a single species *G. settembrinoi,* the body length is a little longer than in the smallest species of *Gerris s. str.* In *Gigantometra* the point for the first segment falls approximately on the growth line for the same segment in *Aquarius,* but the fourth segment falls much above the extended growth line for the same segment of *Aquarius.* The second segment is considerably shorter than the third in spite of the gigantic body size. This suggests that the lengths of these these two segments in *Gigantometra* are realized from quite different growth mechanisms for these two segments from those in *Aquarius* or *Gerris s. str.*

Hoffmann's data on the development of *Limnogonus fossarum* (1936) indicate the highest growth ratio for the first and second segments and lowest for the fourth segment as in *Gerris.* The first segment is only slightly longer than the fourth in a great majority of species of *Limnogonus s. str.,* and the first segment is about twice or at least one and a half times as long as the fourth segment in the subgenus *Limnogonellus.* If growth patterns for the antennal segments similar to those in *Limnogonus fossarum* are shared by the species of *Limnogonellus,* it is expected that the fourth segment would be relatively longer in *Limnogonellus,* which is generally much smaller in body size. Therefore, the relatively short fourth antennal segment in *Limnogonellus* is presumably realized from quite different growth relations between the two segments from those in *Limnogonus s. str.* The allomorphic slopes for the second and third segments in the *Limnogonus s. str.-Limnogonellus* complex, however, appear to reflect the difference in growth ratio between the two segments indicated by Hoffmann's data, *i. e.,* a greater growth ratio for the second segment than for the third segment. In a majority of species of *Limnogonus s. str.,* which are greater in body length, the second segment is longer than the third, while in a few species of *Limnogonus s. str.* (*e. g.,* the smallest species, *L. lundbladi*) and in all species of *Limnogonellus* the second segment is as long as or even a little shorter than the third segment.

In the *Limnometra-Tenagogonus s. str.* complex the incomplete data on *Tenagogonus (Tenagogonus) zambezinus* suggest a gentle proximo-distal gradient of decreasing growth ratio for the antennal segments, but the differences among the segments are very slight. These growth patterns appear to persist to a great measure in the other species of the *Limnometra-Tenagogonus s. str.* complex. As will be noted from the table 15, there is at least no clear tendency for any one segment to be relatively longer or shorter than the other, although the body size varies greatly among species. In *Tenagometrella* (female), *Tenagogonus* (*Tenagometra*), and *Tenagogerris* the fourth segments are considerably shorter than those of the species of the *Limnometra-Tenagogonus s. str.* complex of the corresponding sizes, but the first three segments in these three genera are about equal in length to the same segments in the species of the *Limnometra-Tenagogonus s. str.* complex of corresponding sizes. These facts suggest that the growth patterns for the first three segments in the three genera must be similar to those in the related *Limnometra-Tenagogonus s. str.* complex. In *Tachygerris celocis* (fig. 112) the incomplete growth slopes for the first three segments are steep, and the slope for the fourth segment is much gentler. The allomorphic slope for each segment roughly conforms to the growth slope for each segment except for conspicuous deviations in the third segment of *T. quadrilineatus* and the second segment in *T. spinulatus*. In the male of *Tenagometrella* the antenna is over two and a half times as long as in the female (table 16); the proportional lengths of the first three segments are, however, very similar between sexes. This unusually long male antenna is, therefore, presumably realized primarily from an unusually high initial growth index in the male.

The features common to all genera of this tribe appear to be that the growth ratio for the fourth segment is smallest in all genera except possibly for the *Limnometra-Tenagogonus s. str.* complex, and this segment probably has a high initial size and growth index b. Secondly, there is no conspicuous difference in the steepness of growth slope between the second and third segments, but the growth slope for the second is more often a little steeper than that for the third. Thirdly, there is indication that the more distal segments, especially the fourth, vary more in their growth patterns at the specific level.

Charmatometrini: In one unidentified species of *Brachymetra*, for which incomplete data on the postembryonic development of antennal segments are available, there is a proximo-distal gradient of decreasing growth ratio among antennal segments. In *Brachy-*

metra unca, while the growth slope for the first segment is steeper than those for the other three segments, there is no distinct difference in growth ratio among the last three segments as far as the incomplete data indicate. As noted from figure 114, the growth slope for the first segment is obviously steeper than that for the fourth segment (from a large male nymph to an adult male), and the points for the lengths of both segments of the other species of *Brachymetra, Eobates,* and *Charmatometra* conform fairly well to the growth slopes for both segments (dotted lines represent the slope that would be realized with enlargement of the body in *B. unca*). The first segment in *Brachymetra shawi,* however, obviously deviates. In fig. 113 the postembryonic development of the second and third segments in *B. unca* and the lengths of these two segments in adults are plotted. It is also noted that the allomorphic lines conform fairly well to the growth lines for these segments in *B. unca. Brachymetra lata,* however, deviates greatly from the slope.

All the above facts indicate, apart from a few exceptions, that the species belonging to this tribe have essentially similar growth patterns for the antennal segments. Another fact that deserves mentioning is that in this tribe the growth ratio for the first segment is also much steeper than those for the other segments, as is the case with most genera of Gerrini.

Cylindrostethini: In an unidentified species of *Cylindrostethus* from the Philippines the growth slope (from a large male nymph to a male adult) for the first segment is steepest, and gentlest for the fourth segment; the growth slope for the third segment is only slightly steeper than that for the second (fig. 115). The points representing antennal segments in adults of the other species of *Cylindrostethus* from the Eastern Hemisphere tend to conform less to the growth lines from the more distal segments. *Cylindrostethus sumatranus* ($S_1 — S_4$) makes conspicuous deviations for all segments. This species differs also in the abdominal structures and general color pattern from those in the other congeneric species. In figure 116 the antennal segments in the species of *Cylindrostethus* from the Western Hemisphere are plotted; no nymphal specimens were available for study. It is noted that the allomorphic lines are below and nearly parallel to the corresponding allomorphic lines for the species of *Cylindrostethus* from the Eastern Hemisphere (compare with figure 115). This fact suggests that the two groups of *Cylindrostethus* from different Hemispheres probably differ mainly in the initial growth index b in terms of the allometric equation.

In *Potamobates* a large male nymph specimen of *Potamobates woytkowskyi* was available for measurement. In figure 117 it is immediately noted that the allomorphic slopes for the first and fourth segments conform fairly well to the growth slopes for the corresponding segments. As in *Cylindrostethus,* the slope for the first segment is much steeper than that for the fourth segment. The data indicate also that the growth slopes for the second and third segments are about equally steep, but in both the largest and smallest species (*P. thomasi* and *P. horváthi*) the second segment is distinctly longer than the third; in all other species both segments are about the same in length. The growth patterns for these two segments in these two species may be considerably different from those in other species. As will be pointed out elsewhere, *P. thomasi* deviates also structurally.

In the postembryonic development of the antennal segments in *Platygerris depressus* (from a large male nymph to an adult male, figure 118) the growth ratio for the first segment is greatest and smallest for the fourth segment; the growth ratio for the third segment is a little greater than that for the second segment, as far as the incomplete data indicate. The points representing the segments in other species of *Platygerris* do not conform to the growth lines of *Platygerris depressus* for all segments. Each species must have different growth patterns for antennal segments. This is the only genus of Gerrinae in which the allomorphic lines for the antennal segments do not at all conform to the growth lines. A possibility exists, however, that this is due partly to enormous prolongation of the eighth abdominal segment in the largest species, *Platygerris caeruleus.*

Eotrechini: A large nymph of *Chimarrhometra orientalis* and a large male nymph of *Onychotrechus rhexenor* were available for study. By comparing them with corresponding adults, it was found that the growth slopes for the first segments are steeper than those for the other segments, and the slopes for the fourth segment are gentlest. The lengths of the first segments in all species of the tribe fall approximately on the growth line for the same segment in *O. rhexenor.* The fourth segments in the species of *Amemboa* and *Eotrechus* * fall much above the growth line for the same segment in *O. rhexenor.* The four genera of Eotrechini are not closely re-

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* In the specimen of *Eotrechus kalidasa* Kirkaldy the two distal segments are missing. Distant's figure (1904, p. 104), however, clearly indicates that all segments are very much the same in length. Distant's description says "antennae with the first and second joints longest and subequal, third and fourth a little shorter and subequal."

lated; it is not expected, therefore, that they would have very similar growth patterns for the antennal segments. The number of species available for study is also limited, so that the analysis is difficult.

Ptilomerinae: In two nymphal specimens at different developmental stages of an unidentified species of *Ptilomera* from India (fig. 119), the lines connecting the points for each antennal segment at the three stages are nearly straight on the log-log grid, indicating allometric growth for these segments. It is noted that the lengths of the first segments of different species of *Ptilomera* fall roughly on the growth line for the same segment. The species in the other genera, except for *Rheumatogonus,* also fall close to the growth line for the first segment of the *Ptilomera* species from India. In this subfamily the growth slopes for the first segments in all genera, except *Rheumatogonus,* are presumably much the same. Esaki (1923) thought that in this subfamily the proximal segments of the antennae and legs have been prolonged in adaptation to their peculiar habitat (rapid and turbulent streams). This appears to be true. If the first antennal segments in these genera are plotted on the graph for the hypothetically primitive antennal segment (fig. 127) they fall far above the growth line for the latter. The growth ratio k for the first antennal segment in the species of *Ptilomera* from India is 0.89 and b is 0.05 *. The k value is considerably smaller than that for the same segment in the hypothetically primitive gerrid, with acquisition of the relatively high b value of 0.05. In two species of *Rheumatogonus* studied, the first antennal segments fall close to the hypothetically primitive growth line for the antennal segment. In this subfamily, therefore, the relatively primitive condition for the first segment appears to have been retained in this genus only.

Among the other three antennal segments in the *Ptilomera* species from India, the growth ratios appear to decrease in proximo-distal order. In *Ptilomera* the slopes for all segments apparently are gentler than, for instance, in *Gerris.* In *Potamometra,* which is somewhat related to *Ptilomera,* all segments except for the fourth, fall below the growth lines for the corresponding segments in the *Ptilomera* species studied. Since the number of species in the other genera is highly limited and the developmental data are not available, they are not discussed here. From figures 119 and 120, however, the degree of conformity of the antennal segments to the growth lines in the *Ptilomera* species can be roughly visualized.

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* Comparable with b values in the two species of *Gerris* studied.

Halobatini: Miyamoto's data (1937) on the postembryonic development of *Asclepios coreanus miyamotoi* indicate that the length of the first antennal segment at the fifth nymphal stage is 3.45 times as long as that at the second nymphal stage; comparable figures for the second, third, and fourth segments are 2.33, 2.09, 1.86 times as long as those at the second nymphal stage. To see whether these differences in growth ratios persist in the *Asclepios-Halobates* complex or not, the lengths of antennal segments in adults of the species belonging to these two genera were plotted. It was found that the allomorphic lines for the first and fourth segments roughly reflect the difference in growth ratios between the first and fourth segments in *Asclepios coreanus miyamotoi.*

Metrocorini: In figure 121 the points representing the species of *Metrocoris* (smaller points represents the lengths at nymphal stages in *Metrocoris histrio*), except for the largest species, *Metrocoris stali*(?), conform fairly well to the growth lines for the corresponding segments in *Metrocoris histrio.* A rather sharp decline of growth ratio at the final stage of development, which occurs in *M. histrio,* probably occur in all other species as seen from the fact that all points for the first and fourth segments fall below the growth lines for these segments in *M. histrio* (here represented by regression lines). As already found, the proximo-distal order of decrease of growth ratio is present in *M. histrio* ($P<0.05$) and the growth ratios for the basal segments (male) are peculiarly high in the same species. Similar growth pattern probably exists in many or all species of this genus. It was found by plotting that each segment in the related genera, *Eurymetra, Eurymetropsis* and *Eurymetropsiella,* falls close to the growth line for the corresponding segment in *M. histrio.*

In figure 122 the incomplete growth lines (male) for the first and second segments are steeper than those for the third and fourth segments in *Ventidius henryi.* The degree of conformity of allomorphic lines to the growth lines of the corresponding segments can be seen also from the same figure. In *Esakia* the points for the first segments fall considerably above the growth line for the first segment in *V. henryi.* The second, third and fourth segments fall roughly on the allomorphic lines for these segments in *Ventidius.* In the female of *V. henryi* the growth slope for the third segment is much steeper than that for the fourth, and even a little steeper than that for the second. In *Esakia* the female third segment is also relatively longer than in the male as in

Ventidius. *Esakia,* in this respect, appears to have inherited a similar growth pattern from a *Ventidius*-like ancestor. In *Esakia* the male third segment is greatly thickened and modified as if compensating for its relative shortness.

Rhagadotarsinae: In the postembryonic development of the female antennal segments in *Rheumatobates rileyi palosi* (2nd instar to adult female, figure 123) the growth slopes for the first, third and fourth segments are about equally steep, and they are much steeper than the slope for the second segments. It is noted from the figure that the allomorphic slope for the first segments in the species of Rhagadotarsinae is nearly parallel to the growth slope for the first segment in *Rheumatobates rileyi palosi,* and all points fall on or above the regression line for the postembryonic development of the first segment in the species studied. Most white points representing the second segments in the species of Rhagadotarsinae also fall roughly in the expected areas. The characteristics of growth patterns for the antennal segments in this subfamily are: (1) The growth ratio as well as the initial size of the second segment is much smaller than those of the other segments. (2) There is no great difference in growth ratios among the first, third and fourth segments. (3) There appears to be increase in growth ratio at the final stage of the development for all segments.

Trepobatinae: Figure 124 shows the postembryonic development of the antennal segments in *Trepobates knighti,* together with the first and second antennal segments in the males of the other species of *Trepobates.* The growth lines for the first and second antennal segments in *T. knighti* are expressed by regression lines. Due primarily to the relatively small range in body size among species, the points representing the first and second segments tend to cluster at certain points, thus not suggesting underlying growth slopes. It is, however, interesting to point out that the white points representing the first segments and black points representing the second segments fall above the growth lines (regression lines) for the corresponding segments in *T. knighti.* This is due probably to an abrupt increase in growth ratio at the final stage of development, as evidently occurs in *T. knighti.* As already found, the growth ratio k for the first segment in *T. knighti* is greater than the equivalent in *Gerris,* but smaller than in *Metrocoris histrio.* There is no statistically significant difference in growth ratios among the first three segments, and the growth ratio for the fourth segment is lowest in *T. knighti.*

In figure 125 it is seen that the growth slopes for the antennal segments from a large male nymph to an adult male in *Telmatometra indentata* are much steeper than those in *Trepobates,* and of all segments the third segment is steepest (other unpublished data also indicates that the ratio is greatest for the third segment). As immediately noted, the allomorphic slopes for the first and second segments conform fairly well to the growth lines for the same segments in *T. indentata,* but the same for the third segment does not at all conform to the incomplete growth slope for the same segment in *T. indentata.* The unusually steep growth slope for the third segment in *T. indentata* coupled with this disconformity between the growth and allomorphic lines lead one to suspect strongly that the growth pattern for this segment might be highly variable at the specific level in this genus. Although not shown in the graph, the data indicate the presence of a similar condition for the fourth segment. In *Trepobatoides* (fig. 125) the antennal segments, except for the second, do not at all conform to the growth line for the antennal segments in *Telmatometra indentata.* In *Halobatopsis* the first and second, especially the former, fall approximately on the allomorphic lines for these segments in *Telmatometra.* In *Ovatametra,* no segment, except for the third, falls close to the growth lines for the antennal segments in *Telmatometra indentata.*

In *Metrobates porcus* the growth slope for the first segment based on large male nymph and an adult male, is remarkably steeper than those for the other segments, and the lengths of the first segments in the other species fall on the graph in conformity to the growth line for this segment in *M. porcus* (fig. 126). In spite of a relatively small range in the body size among the species of *Metrobates,* the allomorphic line for this segment well reflects a very high growth ratio common to all species. The allomorphic slope for the second segment is also nearly vertical, but the growth slope for this segment in *M. porcus* is gentle. The allomorphic slope for this segment never reflects the growth slope for this segment in *M. porcus.* The growth slope of the second segment in another species, *Metrobates denticornis,* was found to be even a little gentler than that in *M. porcus.* The nearly vertical secondary allomorphic slope for this segment in *Metrobates* is apparently formed by a high degree of variation in growth pattern for this segment at the specific level, either in the initial growth index or the growth ratio, or both. A similar condition exists for the third segment in this genus. It should be pointed out, however, that the second and third segments in this genus are always provided with a conspicuous comb shaped process at their distal ends. This kind of modification might have something to do with alteration in the growth pattern at the specific level, depending on different degrees of modification.

In *Hynesionella omercooperi* there is a proximo-distal gradient of decreasing growth ratios (from a large male nymph to an adult male). In *Cryptobates* the absolute lengths of the first segment in two species studied are very different (7, 13 micrometer units respectively), but this wide difference can easily be conceived if the growth ratio for this segment is very high as in the other genera of this subfamily, taking into account a considerable difference in body size between the two species (42, 55 units). *Stenobates* and *Rheumatometroides* are monotypic genera but they are closely related. The lengths of the first segments in these two genera are also greatly different (25, 13 units respectively), but if these two genera have a high growth ratio for the first segment as in the other genera, this difference in lengths of the first segments would easily be realized, considering a rather great difference in body size between the two genera (72, 55 units respectively). In *Metrobatopsis* the species are highly variable in degree of structural specialization. Correlated with this, each species appears to have a considerably different growth ratio even for the first segment.

From the above account it is clear that the growth ratio for the first segment is remarkably high in at least a great majority of genera of this subfamily. Whether this high growth ratio is of any adaptive advantage or not is open to question. The species belonging to this subfamily usually live in quiet waters, so the relatively long first antennal segment cannot be adaptively advantageous in the same manner as it is for Ptilomerinae which live in swift and turbulent waters. Assuming, however, that the reduction in body size is also at work in the evolution of this subfamily as in the other subfamilies, this high growth ratio could have been a very efficient mechanism in reducing the absolute as well as relative lengths of the first segment, since they do not need extremely long antennae to maintain themselves on the quiet waters. It should be recalled that the long first antennal segment in Ptilomerinae appears to be realized by a relatively high initial growth index b with a relatively low growth ratio k. Therefore, the relatively long first antennal segment in the larger species of most genera of Trepobatinae and the long first antennal segment in Ptilomerinae (except for *Rheumatogonus*) are quite different both in developmental pattern and adaptive significance.

Evolution of the growth gradients for the antennal segments

In the foregoing accounts various types of growth gradients for the antennal segments in various groups have been observed. The next logical step is to search for a possible growth pattern from which various types of gradients might have been derived.

It was found that the four antennal segments in *Eotrechus kalidasa* are strikingly similar in lengths. It may reasonably be assumed that this condition is the primitive one. The assumption is justified by a general criterion in comparative anatomy which regards the more similar condition among homologous structures as more primitive. Moreover, *Eotrechus* is highly primitive in many structures, probably the most primitive, in an overall sense, in the Gerridae. When many structures are primitive, there is a good possibility that the other structures will also be primitive.

The question next arises as to just how this supposed primitive antenna in *Eotrechus* would be realized in terms of allometric growth mechanisms. In fig. 127 we see that in *Eotrochus kalidasa* and *Tenagogonus (Limnometra) ciliatus*, the first segments fall a little above the extended growth line for that segment in *Onychotrechus rhexenor*, a relatively primitive member of Eotrechini. This suggests that all three species, in spite of their difference in body size and generic status, have similar growth ratios. Since the growth ratio for the first segment, as already shown, is best stabilized at the generic level and the segment in two primitive species falls close to the extended growth line for this segment in *O. rhexenor*, the regression line for the first segments in *Onychotrechus rhexenor*, *Eotrechus kalidasa*, and *Tenagogonus (Limnometra) ciliatus* in fig. 127 can reasonably be regarded as representing the most primitive growth line for an antennal segment in the Gerridae. The growth ratio k for this primitive antennal segment is 1.142. This value is also close to the growth ratio for the first antennal segment in another primitive species, *Gerris (Aquarius) remigis* Say (k is 1.216).

For the realization of similar absolute lengths among antennal segments in *E. kalidasa* a very similar growth pattern for each segment presumably exists. This presumption is justified by the facts that the growth ratios for all antennal segments, except for the third, are similar in Hoberlandt's (1947) data on *Tenagogonus madagascariensis* and in my incomplete developmental data on the antennal segments in *Tenagogonus zambezinus* which indicate similar growth ratios for all segments. Moverover, there is no tendency for any one segment to be relatively longer or shorter than the others in *Tenagogonus,* in spite of the fact that the range of the body length is great among species. The similar absolute lengths among antennal segments in *Eotrechus kalidasa* must be realized by similar growth relations among segments to those in *Tenagogonus.* The hypothetically primitive growth ratio for an antennal segment, therefore, should be valid for all segments.

From the hypothetically primitive growth pattern for all antennal segments outlined above, has evolved the proximo-distal gradient of decreasing growth ratios, as diagrammatically illustrated in fig. 128. In figure 128 type A represents the most primitive condition, in which the growth ratios for all antennal segments are the same ($k = 1.142$). To realize the same or very similar lengths of antennal segments by the same growth ratios for all segments the initial sizes of all segments, or initial growth indices, should be the same or very similar. The growth lines for all segments, thus completely overlap. To see how well the actual growth patterns for the antennal segments in *Eotrechus kalidasa* would conform to this supposed primitive condition remains as an interesting problem to study in the future. *Tenagogonus* is probably near this condition. Type B is the condition in which the growth ratio for the fourth segment alone has been significantly affected. This condition appears to exist in *Gerris s. str., Tenagometra, Tenagogerris, Tenagometrella,* and some species of the *Limnometra-Tenagogonus* complex. The growth patterns in *Trepobates knighti* and *Tachygerris* are similar to those in *Tenagometra, Tenagogerris,* and *Gerris s. str.* in that the growth ratio for the fourth segment only has been greatly lowered, but the growth ratios for the first three segments in *Trepobates knighti* are much greater than in the hypothetically primitive gerrid. Type C is a further affected condition, in which the growth ratios for the last two segments have been lowered in evolution. The growth patterns for the antennal segments in *Gerris (Aquarius) remigis* appear to approximate this condition. Type D is the proximo-distal gradient in decreasing growth ratios. The growth pattern in *Metrocoris histrio* fits this condition, although the growth ratios for the basal segments are very high. Type E is the condition in which the growth ratio for the first segment is very high and the proximo-distal order of decreasing growth ratios is maintained. This condition is suspected to be present in some groups of Trepobatinae. Type F is an exceptional condition in which the growth pattern for the second segment alone has been significantly affected by evolution. This type is present in Rhagadotarsinae.

The hind leg

Gerrini: In figure 129 the growth slopes for the femur, tibia, and tarsus in G. *(A.) remigis* are definitely steeper than those in G. *(G.) marginatus.* (The growth ratios for the tibia and tarsus in G. *(A.) remigis* are greater than the same in G. *(G.) marginatus* at the level of $P. < 0.05$). Note how well the points for adults of various species conform to the growth slopes in each subgenus. Although there are no statistically significant differences in growth ratios between the femur and tibia in either species studied, there is a tendency for the tibia to be shorter in relation to the femur in the smaller species at least in *Aquarius.* It may also be said that the points for tarsi deviate slightly more from the growth lines for corresponding segments in both species. In *Gigantometra* the femur falls a little above the growth line for the segment in G. *(A.) remigis,* but the tibia falls much above and the tarsus considerably below the growth line for the corresponding segments in the same species, suggesting that the growth patterns for these two segments are significantly different from those in *Aquarius.* In the subgenus *Limnoporus* of *Gerris* the points for femora and tibiae fall a little below the growth lines for the corresponding segments in G. *(A.) remigis,* although the points for tarsi fall a little above the growth line for the same segment in G. *(A.) remigis.* The three segments in *Gerriselloides* fall on or very close to the corresponding segments in *Gerris s. str.,* suggesting that this genus has the growth patterns for the hind leg segments very similar to those in *Gerris s. str.* In *Gerrisella* the femur falls quite close to the growth line for the same segment in G. *(A.) remigis,* but the other two fall much below the growth lines for the corresponding segments in both species of the genus *Gerris* studied. Evidence at hand * indicates that the allomorphic slopes in *Eurygerris* do not reflect the growth slopes for the three segments common to all species.

In figure 130 three leg segments in all species of the *Limnometra-Tenagogonus s. str.* complex were plotted. The regression coefficients for the femur, tibia, and tarsus are 1.016, 1.469, 0.846, respectively (these values reflect allomorphic slopes). Hoberlandt's (1947) data on *Tenagogonus madagascariensis,* however, indicate that the length of the femur in adult male is 1.89 times as long as

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* Complete developmental data for two species under study.

that in a second stage nymph; the tibia and tarsus in an adult male are 1.81 and 1.45 times as long as the same segments in a second instar respectively. These growth ratios thus do not coincide with the regression coefficients for the three segments in the *Limnometra-Tenagogonus s. str.* complex noted above. Incomplete data on the growth of the hind leg segments in *Tenagogonus zambezinus* (fig. 130) also show a similar growth pattern to that in *T. madagascariensis.* In fact, as will be noted from figure 130, there is a tendency for the growth slopes of the segments in *T. zambezinus* to deviate progressively more in the more distal segments from the allomorphic slopes of the corresponding segments. The absence of coincidence between the allomorphic and growth slopes for the corresponding segments might have resulted from a progressive decrease in growth ratios for the more distal segments in the smaller species (*Tenagogonus s. str.*), or from a decrease in initial growth index with growth ratio remaining unchanged in the smaller species. Whatever the underlying mechanism may be, the tibia is relatively shorter in the smaller species, resulting in the formation of the steeper secondary allomorphic slopes for the tibia than for the femur. The three hind leg segments in the genera or subgenera related to the *Limnometra-Tenagogonus s. str.* complex (*Tenagometra, Tenagometrella* and *Tenagogerris*) fall close to the regression lines for the corresponding segments in the *Limnometra-Tenagogonus s. str.* complex.

In figure 131 are shown the growth lines for the femur and tibia in males of an unidentified species of *Limnogonus* (from a large nymph to an adult female) from New Guinea. All points for the other species are leg segments in the females in this genus. It is immediately noted that the deviation of the points for the tibia (round points for *Limnogonus s. str.*, triangles for *Limnogonellus*) from the incomplete growth line for the same segment is greater than the same for the femur. The same interpretation as given above for the *Limnometra-Tenagogonus s. str.* complex can be made for the greater deviation of the points for tibiae from the growth line for this segment. Evidence at hand (two species representing both subgenera, under study) indicates, however, that the growth patterns for the tibia in these two species is similar. Apart from the underlying growth mechanisms, the tibia is shorter in relation to the femur in the smaller species, as suggested by the steeper allomorphic slope for the tibia than that for the femur. *Limnogonus intermedius* is represented by × in figure 131. Note how the leg segments in this species deviate from the corresponding allomorphic lines for the other species. This species, together with a few other African species, deviates also in other characters.

In figure 132 the allomorphic slopes for the tibia and tarsus do not conform to the growth slopes for the same segments in *Tachygerris celocis.* The growth slopes for the same segments in *Tachygerris spinulatus,* which is larger in size, are much gentler than those in *T. celocis.* These incomplete data suggest that the disconformity of allomorphic slopes to the growth slopes for the tibia and tarsus apparently results from the difference in growth pattern among species. The difference in growth slope for the femur between *T. celocis* and *T. spinulatus* is much less than the differences in the other two segments between the two species, and the allomorphic slope for the femur conforms fairly well to the growth slopes for this segment in the two species. The secondary allomorphic slope for the tibia is steeper than the allomorphic slope for the femur as in the other genera, and the tibia in the shorter species is also relatively shorter in this genus.

Charmatometrini: In figure 133 E, E′ represent a nymph and an adult (male) of an unidentified species of *Brachymetra* from Ecuador and P, P′ represent a nymph and an adult (male) of an unidentified species of *Brachymetra* from Panama. The allomorphic slopes deviate more from the growth slopes in the more distal segments. The allomorphic lines appear to be formed by smaller growth ratios for all segments in the shorter species. Although the growth ratio for the femur is about as great as or a little greater than that for the tibia in all three species, the secondary allomorphic slope for the tibia is even a little steeper than that for the femur, due apparently to a little greater degree of alteration in growth pattern for the tibia at the specific level. The tibia and tarsus are thus relatively shorter in the shorter species in Charmatometrini.

Cylindrostethini: In figure 134 the allomorphic lines for the femur and tibia in the species of *Cylindrostethus* from the Eastern Hemisphere (triangle points) conform well to the growth lines for the corresponding segments in an unidentified species of *Cylindrostethus* from the Philippines. The allomorphic lines for the femur and tibia in the Western Hemisphere species of *Cylindrostethus* (round points) are nearly parallel to the equivalents in the Eastern Hemisphere species of *Cylindrosthethus.* If these very similar allomorphic slopes for the femur and tibia in the two groups of *Cylindrostethus* really reflect the similarity in the growth slopes for the segments between the two (no developmental data are available for the Western Hemisphere species of *Cylindrostethus*), the difference between the two groups lies primarily in the initial growth index b in allometry equation terms, *i. e.*, a lower b value for the Western Hemisphere *Cylindrostethus* than that for the Eastern Hemisphere *Cylindrostethus.* The growth line for the tarsus is a little steeper than the allomorphic line for the same segment in the Eastern Hemisphere species of *Cylindrostethus.* The tarsus tends to be longer in the smaller species of Western Hemisphere *Cylindrostethus.* It is thus most improbable that the different lengths of tarsi in different species have been derived from a similar growth mechanism common to all species. Since the growth, as well as the allomorphic, slopes for the tibia are steeper than those for the femur, the tibia is relatively shorter (in relation to the femur) in the smaller species in this genus, as in the other genera of Gerrinae.

In figure 135 incomplete postembryonic growth lines for the femur and tibia in *Potamobates horváthi* and the lengths of three leg segments in all species of *Potamobates* are plotted. Note how well the segments, in all species except for *Potamobates thomasi,* conform to the growth lines for the femur and tibia in *P. horváthi.* All species, except for *P. thomasi,* probably have much the same growth patterns for these segments. It should be recalled that *P. thomasi* deviates also in the lengths of antennal segments. The tarsus is missing from the nymph studied. Both the growth and the allomorphic slopes for the tibia in this genus are steeper than those for the femur, and the tibia is also relatively shorter in the smaller species.

In *Platygerris,* it was found that the allomorphic lines do not at all conform to growth lines for all segments in *Platygerris depressus;* they rather greatly deviate from the latter, as will be noted from figure 136. The growth slope for the femur is much steeper than the same for the tibia in *P. depressus.* In almost all genera of Gerrinae the middle and hind femora are about as long as the body, but in this genus they are considerably longer than the body, probably in correlation with their habitat in rapidly running water. These rather extraordinarily long femora are apparently realized from this very high relative growth ratio. *Platygerris* offers a unique case in which the allomorphic slope for the femur is so much different from the growth slope, but this is partly due to extraordinary development of the eighth abdominal segment in the largest species, *P. caeruleus.* The secondary allomorphic slope as well as the growth slope (in two species under study) for the tibia are steeper than those for the femur, and the tibia is relatively shorter (in relation to the femur) in the smaller species.

Eotrechini: The growth lines from a large male nymph to an adult male for the femur and tibia in *Chimarrhometra orientalis* and *Onychotrechus rhexenor* are nearly parallel to each other. The growth line for the tarsus in *O. rhexenor* is nearly horizontal. Whether allomorphic slopes coincide with growth slopes or not is difficult to see for the reasons mentioned previously. At the generic level, however, there is a tendency for the tibia to be relatively longer in the more primitive and larger (in size) genera. In the largest (in body length) and structurally very primitive genus, *Eotrechus,* the tibia is even longer than the femur. In *Onychotrechus* the tibia is longer in relation to the femur than it is in *Amemboa,* which is smaller in body size and generally more specialized structurally. This tendency, however, is probably realized from different growth patterns in different genera, since the four genera are not closely related to each other. It is interesting to recall that in the largest and structurally most primitive species of Gerrini, *Gigantometra gigas,* the tibia is also much longer than the femur, as in the largest species in Eotrechini, *Eotrechus kalidasa.*

Ptilomerinae: Since the tibia and tarsus in dried museum specimens of this subfamily are always greatly twisted, the study of these two segments is not attempted. The femur, however, is always robust and straight. In figure 137 is shown the incomplete postembryonic development of the femur and tibia at three different developmental stages in an unidentified species of the genus *Ptilomera* from Southern India. The femora in all other species of *Ptilomera,* except for one, fall very close to the growth line for the femur. This beautiful conformity suggests that the growth pattern for the femur is much the same in most species of *Ptilomera* studied. Note also the steeper growth slope for the tibia than that for the femur. It was found by plotting that the femur of *Potamometra berezowskii* falls considerably above the growth line for the femur in the *Ptilomera* species from India. The femora in *Rhyacobates, Heterobates, Potamometropsis, Potamometroides,* and *Rheumatogonus* come below the line. *Rheumatogonus* has the shortest femur as is the case with the first antennal segment, and this is probably the least specialized condition in Ptilomerinae. In all species of Ptilomerinae, however, the hind femur is longer than the length of the body, and this is presumably the prerequisite for them to survive swift and turbulent currents by maintaining their body with the aid of relatively long proximal antennal and leg segments. In Gerrinae it is only in *Platygerris,* which inhabits similar streams, that the femur is longer than the body. In this subfamily (at least in *Ptilomera*), in contrast to *Platygerris,* the relatively long femur is apparently realized by a rather gentle growth slope, gentler than that for the tibia, with probably a large initial size, or initial growth index in terms of the allometry equation.

Halobatini: Miyamoto's data (1937) on *Asclepios coreanus miyamotoi* indicate that the growth ratio for the tibia is a little greater than that for the femur (5th instar femur : 1st instar femur : : 72-23, 5th instar tibia : 1st instar tibia : : 40:12), the growth ratio for the tarsus is much smaller than those for the other two segments (5th instar tarsus : 1st instar : : 15.5:8). In figure 138 it is noted that regression lines for the femur and tibia would be nearly parallel. *Halobates proavus* deviates conspicuously, especially for the tibia and tarsus. The allomorphic slope for the tarsus is much gentler than those for the two preceding segments. The differences among allomorphic slopes thus roughly coincides with the differences in growth ratios among the three segments in *A. coreanus miyamotoi.*

Metrocorini: In *Metrocoris* the points representing the femora and tibia in all species, except for the largest, *Metrocoris stali*(?), fall below and along the growth line for each segment in *Metrocoris histrio* (fig. 139 represented by regression lines). This reflects a possible abrupt decrease in growth ratio at the final stage of development in all species, which evidently occurs in *M. histrio* as seen from the figure. The allomorphic line for the tarsi considerably deviates from the growth line for the same segment in *M. histrio.* All segments in *Eurymetra, Eurymetropsis,* and *Eurymetropsiella* fall roughly on the allomorphic lines for the corresponding segments in *Metrocoris.* As in *Gerris (Aquarius) remigis,* there is no statistically significant difference in growth ratio between the femur and tibia in *M. histrio.* Similar growth relations probably exist in the other genera related to *Metrocoris.*

In figure 140 the points representing the femora in *Ventidius* fall close to the growth line for the femur of *Ventidius henryi.* For the tibia all species, except for *Ventidius malayensis,* conform very closely to the growth line for the same segment in *V. henryi.* Due to a great deviation of the tibia in *V. malayensis* the allomorphic line for the tibia is steeper than that for the femur. For the tarsus

V. malayensis also greatly deviates. It was found that the femur in two species of *Esakia* fall a little above the allomorphic slope for the femur in *Ventidius;* the other two segments in *Esakia* come close to the corresponding segments in *Ventidius.*

In Metrocorini the allomorphic slope for the femur is closest to the growth slope for the same segment. The allomorphic slope, however, tends to deviate more from the growth slope in the more distal segments, as is the case with some genera of Gerrinae. Because of this tendency the tibia is shorter in relation to the femur in the smaller species of some genera.

Rhagadotarsinae: In figure 141 the complete growth lines of leg segments in *Rheumatobates rileyi palosi* (female), and the incomplete growth lines in *Rhagadotarsus (Caprivia) hutchinsoni* (female) together with points representing the leg segments in all other species of the subfamily (female) are shown. In *Rheumatobates* the size of the body does not vary much among a majority of species, so that the points tend to cluster within a certain area, but the essential conformity of the points to the growth lines for the femur and tibia is evident from the fact that the points for both the smaller and larger species are roughly on the growth lines for the corresponding segments. The points for tarsi obviously deviate from the growth line for the same segment in *Rheumatobates rileyi palosi.*

As already found, there is a proximo-distal gradient of decreasing growth ratio ($P<0.05$) in *R. rileyi palosi.* The incomplete growth lines for the three segments in *Rhagadotarsus (Caprivia) hutchinsoni* also indicate the same order of decrease in growth ratio as in *R. rileyi palosi.* Hoffmann's data (1936) on the postembryonic development of the hind leg segments in *Rhagadotarsus (Rhagadotarsus) kraepelini* also indicate the same order of decrease in growth ratio, *i. e.*, the femur at the fifth nymphal stage is five times as long as the same at the first nymphal stage; the tibia and tarsus at the fifth stage are 3.4 and 2.06 times as long as the same at the first nymphal stage. This ontogenetic evidence representing all major groups of this subfamily, in turn, indicates that the proximo-distal gradient of decreasing growth ratio for the hind leg segments is probably widely prevalent in this subfamily. There is a good possibility, however, that the growth ratio for the tarsus is considerably different at the specific level. It is important also to point out that the difference in growth lines for the femora between the two species (*R. (C.) hutchinsoni* and *R. rileyi palosi*) is less than the difference in growth lines for the other two segments between the two species, suggesting that the growth pattern for the femur has been more well fixed than the other segments in this subfamily. The same tendency was already observed in the other subfamilies of the Gerridae. Another important matter is that most points representing the tibiae and femora fall above the growth line (regression line) for each segment. This is apparently due to an abrupt increase in growth ratio at the final stage of development for the segments, as evidently occurs in *Rheumatobates rileyi palosi.* Because of the proximo-distal gradient in growth ratio for the three segments there is no tendency for the tibia to be shorter in relation to the femur in the smaller species.

Trepobatinae: In figure 142 is shown the complete postembryonic development for the three segments in *Trepobates knighti.* It is immediately noted that in this species also the growth slope for the femur is steepest and that for the tarsus gentlest as in Rhagadotarsinae, although there is no statistically significant difference in growth ratio between the tibia and tarsus. The points representing the leg segments in other species within the genus also conform fairly well to the growth lines. Due to a small range in body sizes among species in this genus the points tend to aggregate within a certain area, but at least no conspicuous deviation is noted. As in the case with the femur and tibia in Rhagadotarsinae, all points representing the leg segments fall above the growth lines for the corresponding segments (here represented by regression lines). This is apparently due to an abrupt increase in growth ratio at the final stage of development, which evidently occurs at least in *T. knighti.* Because of the growth patterns noted above there is a tendency for the tibia to be relatively longer in the smaller species in this genus. *Trepobatoides boliviensis* and *Telmatometra ujhelyi* were also plotted on the same graph to show that in both species the lengths of femora and tibiae fall considerably above the growth lines for the corresponding leg segments in *T. knighti.*

In figure 143 the growth slope for the femur is steepest and gentlest for the tarsus in *Telmatometra indentata* (from a large nymph to an adult male). The allomorphic line for the femur closely conforms to the growth line for the same segment in *T. indentata,* with a slight deviation in *Telmatometra retusa.* The allomorphic slopes for the tibia and tarsus, however, are very much steeper than the growth slopes for the corresponding segments. In the same figure the growth slopes for the femur and tibia are nearly parallel, and steeper than the growth slope for the tarsus in *Halobatopsis spiniventris* (from a large male nymph to an adult male). While the points for the femur fall on the growth line in *H. spiniventris* the line connecting the tibae and the one connecting tarsi in two species of *Halobatopsis* (allomorphic lines) are much more vertical than the growth lines for these segments in *H. spiniventris,* as in the genus *Telmatometra.* The growth slopes for the femur is steeper than that for the tibia in *H. spiniventris.* In these two genera there is a tendency that the allomorphic slopes deviate from the growth slopes for the corresponding segments more in the more distal segments. In *Ovatametra* the femur and tarsus do not fall close to the allomorphic lines for these segments in *Telmatometra* and *Halobatopsis.*

In figure 144 the incomplete growth lines for the femur and tibia are nearly parallel in *Metrobates denticornis,* although the growth slope for the femur is steeper than that for the tibia in another species, *Metrobates porcus.* While the points for the femora fall close to the growth lines for the femur in both species, the allomorphic slopes for the tibiae and tarsi are nearly vertical and deviate greatly from the growth lines for the corresponding segments. As will be noted from figure 144, the difference in the growth slopes for the femur between the two species is very slight, but the difference is much greater for the other two segments. This strongly suggests that the growth ratios for the tibia and tarsus may vary greatly at the species level in *Metrobates.* We have already observed a similar tendency for the second to fourth antennal segments in the same genus. As in *Telmatometra* and *Halobatopsis,* the allomorphic slopes for the tibiae and tarsi are thus much steeper than that for the femur.

The proximo-distal gradient of decreasing growth ratios for the hind leg segments was found in *Hynesionella omercooperi* on the basis of incomplete data on the development (from a large male nymph to an adult male, fig. 145). In *Rheumatometra philarete* the growth slope (from a large female nymph to an adult female) for the tibia is steeper than that for the femur. This is the only trepobatine studied in which the tibial growth slope is steeper than the femoral (note that the data are incomplete and based on females instead of males). In figure 146 the allomorphic slopes for leg segments in *Stenobates biroi* and *Rheumatometroides browni* are much like typical growth lines in Trepobatinae. This suggests that they possibly have similar growth patterns for the hind leg segments, assuming that the growth slopes coincide well with the allomorphic slopes for all segments. In fact these species are closely related. In the same figure, the allomorphic slopes for the leg segments in two species of *Cryptobates* are like typical allomorphic lines in Trepobatinae. In *Metrobatopsis* the data indicate that even the allomorphic slope for the femur does not reflect a probable growth slope for any one species of the genus, although no developmental data are available.

The mechanism of allomorphosis for the hind leg segments

It has become evident from the foregoing discussion that the allomorphic slope for the tibia is almost always steeper than that for the femur. It has become apparent further that the underlying growth mechanism by which the allomorphic slope is formed varies in different groups of the Gerridae. In figure 147 A is diagrammed the condition in which the allomorphic slope is identical with the growth slope for each segment (femur and tibia). To realize this condition all species (A, B, C) must have the same growth ratio and the same initial growth index for these two segments. A condition similar to this probably exists in some genera of Gerrini, etc. Type B is the condition in which the allomorphic slope is the same as the growth slope for the femur, but the growth ratio for the tibia is different at the specific level, *i. e.,* higher growth ratios and lower initial growth indices in the larger species. The allomorphic line (secondary, a in the figure) thus obtained does not represent the growth line for the tibia in any one species, A, B, C. Type C is another condition by which the secondary allomorphic slope for the tibia is formed, *i. e.,* by the lower growth ratios with higher initial growth indices in the larger species. The type B and C apparently occur in various groups of Gerridae. The type D is an exceptional condition in which the growth patterns for the femora are different with those for tibiae remaining much the same among species. This condition was observed in *Platygerris.* Types E and F are the conditions in which the initial growth indices are more or less greatly different while the growth ratios remain much the same among comparable species. If there is a tendency for the initial growth index to be smaller in larger species while the growth ratio remains the same, a nearly horizontal secondary allomorphic slope will be formed as shown in E. This is apparently the mechanism by which the nearly horizontal secondary allomorphic slopes are formed in *Eurygerris.* If, however, there is a tendency for the initial growth index to be greater in larger species than in smaller species while the same growth ratio is present among the comparable species, a nearly vertical or very steep secondary allomorphic slope will be formed (type F).

The middle leg

In figure 148 a majority of points representing the middle leg segments in adults of various species of both subgenera of *Gerris* roughly fall on the growth lines for the corresponding segments. Among the species of *Gerris s. str.* the segments of *G. (G.) gillettei* deviate considerably from the growth lines for the corresponding segments in *G. (G.) marginatus.* In the subgenus *Limnoporus* of *Gerris* the points for femora and tibiae come below the growth lines for the corresponding segments in *G. (A.) remigis.* In *Gigantometra,* both the femur and tibia, especially the latter, fall much above the growth lines for these segments in G. *(A.) remigis,* and the tarsus falls roughly on the growth line for the same segment in *G. (A.) remigis.* In *Gerrisell*a the femur and tibia fall above the regression lines (growth lines) for these segments in *G. (G.) marginatus.* Apparently, there are quite different growth patterns for these segments in two genera *(Gigantometra* and *Gerrisella)* from those in *Gerris.* In *Gerriselloides* all three segments fall close to the growth lines for the three segments in *G. (G.) marginatus,* indicating that this genus has the growth patterns for the middle leg segments very similar to those in *Gerris s. str.* In *Eurygerris* (fig. 148) very gentle secondary allomorphic slope for the femur is apparently formed by more or less great difference in initial growth indices while the growth ratio remains practically the same among species.

In the *Limnometra-Tenagogonus s. str.* complex (fig. 149) the points representing femora and tibiae conform much more closely to the incomplete growth lines for these segments in *Tenagogonus zambezinus* than do the points for the hind leg segments in the same species. Hoberlandt's data on *Tenagogonus madagascariensis* (1947) suggest that the femur grows a little more rapidly than the tibia (femur in adult : femur in 2nd instar :: 181:103; tibia in adult : tibia in 2nd instar :: 140:88), and the tarsus grows most slowly (tarsus in adult : tarsus in 2nd instar :: 67:43). These growth ratios appear to conform roughly to the differences in allomorphic slopes among segments. The nearly horizontal growth line from a large nymph to an adult male in *T. zambezinus* is due possibly to an abrupt decrease in growth ratio at the final stage of development, so the difference in growth ratio for the tarsus between *T. zambezinus* and *T. madagascariensis* may be discounted. In three genera related to the *Limnometra-Tenagogonus* complex, *Tenagometra, Tenagometrella,* and *Tenagogerris,* the three leg segments roughly fall on the allomorphic lines for the corresponding segments in the *Limnometra-Tenagogonus s. str.* complex. In *Tachygerris* (fig. 150) the allomorphic lines for all three segments conform to the growth lines of the corresponding segments much better than in the hind leg.

In figure 151 are plotted three middle leg segments in females of the *Limnogonus s. str.-Limnogonellus* complex. The allomorphic lines for all segments roughly reflect the growth lines for the corresponding segments in two species representing two subgenera of *Limnogonus* now under study. Note the deviation in *L. intermedius* (×).

Charmatometrini: In figure 152 the black points representing the femora in Charmatometrini fall along the incomplete growth line for the same segment in *Brachymetra unca*, the white points for the tibiae in the two smallest species deviate from the growth line for the same segment in *B. unca.* The growth slopes for the femora are evidently steeper than those for the tibiae in the two species studied. If this growth pattern persists among the species of this tribe, the relatively long femora in the larger species will be realized. This appears to be the case in this tribe. The femur is longer than the tibia in only two large species (*Charmatometra bakeri* which is the largest and *Eobates vittatus*); in all others the tibia is longer than the femur. The growth patterns for the femur and tibia in this tribe are essentially similar to those in *Gerris,* in which also the growth slope for the femur is steeper than that for the tibia ($P<0.05$ in *G. (A.) remigis,* $P<0.1$ in *G. (G.) marginatus*). Only because of the relatively small body size in this tribe is the relatively long femur (longer than the tibia) realized in the two large species. In *Gerris,* which is larger in body size than *Charmatometrini* generally, the femur is always longer than the tibia. The allomorphic slope for the tarsus deviates greatly from the growth lines for the same segments in the two species, and this deviation results probably from considerable difference in growth pattern for this segment among species.

Cylindrostethini: In the species of *Cylindrostethus* from the Eastern Hemisphere (fig. 154) the allomorphic slopes for all three segments conform fairly well to the incomplete growth slopes for the corresponding segments in an unidentified species from the Philippines, suggesting that the growth patterns for all three segments are similar in all species. In the group of species of *Cylindrostethus* from the Western Hemisphere the allomorphic slopes, except that for the tarsus, are nearly parallel to those for the Eastern Hemisphere species of *Cylindrostethus,* and they always fall below those for the Eastern Hemisphere *Cylindrostethus,* indicating lower initial growth indices for them. We have already seen similar conditions for the antennal and the hind leg segments in this genus. In *Potamobates* (fig. 155), except for *P. thomasi,* the allomorphic slopes conform fairly well to the incomplete growth slopes in the two species of *Potamobates* studied. In *Platygerris* (fig. 156) the disconformity of the allomorphic line for the femur to the growth line for the same segment in *P. depressus* is conspicuous, although the allomorphic line for the tibia almost overlaps the growth line for the same segment. The middle femur is considerably longer than the body but a little shorter than the hind femur in this genus. This long middle femur appears to be realized by a relatively high growth ratio for the femur, as noted from figure 156. Also the growth pattern for the segments probably differs greatly in the largest species, *P. caeruleus,* as appears to be the case with the hind leg segments in this genus.

Eotrechini: The femur and tibia in *Eotrechus kalidasa* do not fall close to either one of the incomplete growth slopes for these segments in *Chimarrhometra orientalis* or *Onychotrechus rhexenor* (fig. 153). The allomorphic lines for the middle leg segments in all genera are not obtainable or difficult to obtain, due to few species of each genus available for study, or to a small range in body length when sufficient numbers of species are available for study (*Amemboa,* represented by triangles).

Ptilomerinae: In figure 157 the points for the femora and tibiae, except those in *P. werneri,* conform fairly well to the incomplete growth line for each segment in the *Ptilomera* species studied. Deviation of the allomorphic slope for the tibia from the growth slope for the same segment is due partly to inaccuracy in measurement. The middle tibia in dried museum specimens of this genus is difficult to measure for the reasons mentioned previously. In *Potamometra berezowskii* the points for these two segments come above the allomorphic slopes for the corresponding segments in *Ptilomera.* In *Rhyacobates, Heterobates, Potamometroides,* and *Potamometropsis* the points for both segments come below the slopes of the corresponding segments in *Ptilomera*. In *Rheumatogonus* the points for both segments, as might be expected, fall much below the growth lines for the two segments in the *Ptilomera* species from India. The growth slopes for the femur and tibia are apparently gentler than the equivalents in the Gerrinae, and the growth slope for the tibia is a little steeper than that for the femur in the species of *Ptilomera* studied.

Halobatini: In figure 159, while the points for the femora form a nearly straight slope, there is possibly no high correlation between the tibia and the length of body. This is due probably to the presence of a conspicuous mass of hairs on this segment. To carry a mass of hairs of varying degrees of development and density, different species probably have acquired different growth patterns for this segment. The points for the tarsi fall nearly parallel to the allomorphic slope for the femur. The conspicuous mass of hairs occur also on the first tarsal segment in the species of *Halobates*, but not in *Asclepios*. Miyamoto's data (1937) on *Asclepios coreanus miyamotoi* indicate that the femur grows much more rapidly than the tibia or than the tarsus. The nearly parallel allomorphic slopes of the femur and tarsus do not reflect the growth slopes for these segments in *Asclepios coreanus miyamotoi*.

Metrocorini: In *Metrocoris histrio* (fig. 158) the points for all segments, except those for the femur and tibia in *Metrocoris stali*(?), conform fairly well to the growth slopes in *M. histrio*. The points for all leg segments fall below growth lines (regression lines), although the decrease in growth ratio at the final stage of development is not as pronounced as it is for the hind femur and tibia. All three segments in *Eurymetra natalensis* fall roughly on the allomorphic slopes for the corresponding segments in *Metrocoris*. The femur in *Eurymetropsiella* and *Eurymetropsis* fall above the allomorphic line for the femur in *Metrocoris*.

In figure 160 the allomorphic lines for the femur and tibia, except for the femur of *Ventidius malayensis*, conform fairly well to the growth lines for these segments in *Ventidius henryi*. The points for the tarsi also form a slope nearly parallel to those for the preceding segments. Whether this allomorphic slope reflects the growth slope for this segment in *Ventidius* or not remains to be investigated (the tarsus is missing from the nymphal specimen of *V. henryi* available for study). In *Esakia* the points for femora and tibiae in the two species, especially those for the latter segments, come considerably above the allomorphic slopes for these segments in *Ventidius.*

Rhagadotarsinae: In figure 161 the growth lines as well as the points representing leg segments are for the female in the two genera of *Rhagadotarsinae.* While the points for the femora in *Rheumatobates* conform fairly well to the growth line for this segment in *Rheumatobates rileyi palosi,* the tibia in three species (*Rheumatobates crassifemur esakii, Rheumatobates klagei, Rheumatobates bonariensis*) deviate conspicuously from the growth line for the tibia in *R. rileyi palosi.* A great majority of points for the tibiae and tarsi fall above the growth line for each segment in *R. rileyi palosi.* This is due probably to an abrupt increase in growth ratios at the final stage of development, as an abrupt increase in growth ratio at this stage in *R. rileyi palosi* suggests. The deviations of the tarsi in some species are greater than those in the other segments. The three segments in *Rhagadotarsus (Caprivia) hutchinsoni* considerably deviate from the growth lines for the corresponding segments in *R. rileyi palosi.* These deviations probably result from the gentler growth slopes for all segments in this species, as will be noted from figure 161. The growth ratios for the femora and tibae in both *Rheumatobates rileyi palosi* and *Rhagadotarsus kraepelini* (Hoffmann 1936) are about the same (no statistically significant difference between the two segments at the level of $P.<0.05$ in *Rheumatobates rileyi palosi*).

Trepobatinae: In figure 162 the points for the tibiae fall nearly parallel to and above the growth line for the same segment (regression line) in *Trepobates knighti,* due probably to an abrupt increase in growth ratio for this segment at the final stage of development, as an abrupt increase in growth ratio at the final stage of development in *T. knighti* suggests. The points for femora fall considerably above the growth line for the same segment in *T. knighti* due probably to increase in growth ratio at the final stage of development. The points for tarsi (white points), however, fall roughly on the growth line for this segment in *T. knighti,* and the growth ratio for this segment does not increase abruptly at the final stage of development. In *Trepobatoides boliviensis* the points for the femur and tibia are above the allomorphic lines for the corresponding segments in *T. knighti.* In the same figure all segments in *Telmatometra ujhelyi* fall close to the growth lines for the corresponding segments in *T. knighti.*

In figure 163 the allomorphic slope for the femora in *Telmatometra* deviates considerably from the growth line for the same segment in *Telmatometra indentata;* the slope for the tibiae, in all species except for *Telmatometra retusa,* nearly conforms to the growth line for the tibia in *T. indentata;* for the tarsus the allomorphic slope for all species, except for *T. retusa,* cannot possibly be said to conform to the growth line for the tarsus in *T. indentata.* In the same figure the allomorphic slopes for the three segments in *Halobatopsis* may well be said to conform to the incomplete growth slopes for the corresponding segments in *Halobatopsis spiniventris.* In both species, for which incomplete data on the development of leg segments are available, the tibia apparently grows more than the femur. In the same figure the three segments in *Ovatametra minima* come below the growth lines for the corresponding segments in *Telmatometra indentata.*

In figure 164 the allomorphic slope for femora in the species of *Metrobates* conforms roughly to the incomplete growth line for the same segment in *Metrobates porcus.* The allomorphic lines for tibiae and tarsi, however, deviate greatly from the incomplete growth lines for the same segments in two species of *Metrobates* studied. The incomplete growth lines for the tibiae and femora are nearly parallel. In *Rheumatometra* (female) and *Hynesionella* the incomplete growth slopes for the tibiae are steeper than those for the femora.

The growth ratio for the tibia is greater than that for the femur in *Trepobates knighti* ($P<0.05$), and similar growth relations between the two segments probably exist in the other genera of Trepobatinae, as most of the incomplete data on the growth of these two segments indicate. The relatively short and robust femur (always shorter than the tibia) in Trepobatinae is probably realized from this peculiar growth relation between the two segments.

Throughout the major groups of Gerridae the allomorphic slopes for the middle leg segments usually conform much better to the growth slopes for the corresponding segments than do the allomorphic slopes for the hind leg segments to the growth slopes for their corresponding segments.

The front leg

Gerrini: There is no statistically significant difference in growth ratio between the femur and tibia in both species of *Gerris* studied. The growth ratios for both segments in *Gerris (Aquarius) remigis* are, however, considerably greater than those in *Gerris (Gerris) marginatus* ($P.<0.01$). These differences in the growth ratio between the two species are well reflected by the allomorphic slopes for the corresponding segments in each subgenus (fig. 165). In the subgenus *Limnoporus* of *Gerris* the points for the femora and tibiae fall below the growth lines for the corresponding segments in *G. (A.) remigis*, and above those in *G. (G.) marginatus*, and the points for the tarsi fall below the growth line for the same segment in *G. (A.) remigis.* In *Gerriselloides* the points for the three segments fall roughly on the growth lines for the corresponding segments of *Gerris (Gerris) marginatus.* In *Gerrisella* the point for the femur falls a little above the growth line for the same segment in *G. (G.) marginatus.* In *Gigantometra* the three segments fall roughly on the growth lines for the corresponding segments in *G. (A.) remigis.* In *Eurygerris* the lengths of femora in different species are not well correlated with body sizes. This appears to have something to do with a high degree of modification of the inner margin of the femur in males of the smaller species. For example, in the smallest species, *Eurygerris flavolineatus*, the femur is unusually long in comparison with the tibia. In the *Limnogonus s. str.-Limnogonellus* complex also, the allomorphic slopes for femora and tibiae are nearly parallel, and this probably reflects the typical growth slopes for these two segments in the *Limnogonus s. str.-Limnogonellus* complex. In the *Limnometra-Tenagogonus s. str.* complex the front leg segments are considerably longer than in *Gerris* or *Limnogonus*, although the general size of the body is about as large as in the former genus. The points for the femora and tibiae form nearly straight parallel slopes; the slope for the tarsi is also about as steep as that for the two preceding segments. In the related genera, *Tenagogerris, Tenagometra,* and *Tenagometrella* (female), the points for all three segments fall roughly on the allomorphic slopes for the corresponding segments in the *Limnometra-Tenagogonus s. str.* complex. In *Tachygerris* the growth as well as allomorphic slopes are steeper than in the other genera, as in the other legs and the antenna.

Charmatometrini: The allomorphic slopes for the three segments are steeper than the incomplete growth slopes for these segments in the two species of *Brachymetra* studied.

Cylindrostethini: The points for three segments in the species of *Cylindrostethus* from the Eastern Hemisphere fall a little above the growth lines for the corresponding segments in a species of *Cylindrostethus* from the Philippines. The points for the three segments in the species of the Western Hemisphere *Cylindrostethus* fall nearly parallel to the allomorphic lines for the corresponding segments in the Eastern Hemisphere *Cylindrostethus* species, but they come definitely below the latter, as in all other leg and antennal segments. In *Potamobates* all three segments in all species including *P. thomasi*, which deviates otherwise, fall close to or on the growth lines for the corresponding segments in *P. woytkowskyi.* It was found that the incomplete growth lines for all three segments in *P. horváthi* are nearly parallel to those in *P. woytkowskyi.* The front leg segments are relatively short in *Platygerris.* In *Platygerris* the three segments in *P. asymmetricus* fall exactly on the extended growth lines for the corresponding segments in *P. depressus,* while the points for the segments in the largest species, *P. caeruleus,* fall considerably below the extended growth lines of *P. depressus.* We have already seen the deviations of the points for the middle and hind femora and the first antennal segment in this species. This largest species is apparently different in the growth patterns for most leg and antennal segments from those of the other two species of *Platygerris.*

Eotrechini: In *Amemboa* there is apparently no high correlation between the body length and the length of the front leg segments. For example, the femur and tibia are longest in one of the smallest species, *A. horváthi.* The absence of a high correlation has apparently something to do with more or less conspicuous modification on the inner margins of the femur and tibia in the smaller species (fig. 605). A very similar tendency for the front leg in *Eurygerris,* in which also more or less conspicuous modification occurs on the femur in the smaller species, was already noted. Since the number of species per genus is limited in the other genera, they are dismissed here.

Ptilomerinae: In figure 166 the allomorphic slopes for the three segments in *Ptilomera* conform fairly well to the growth lines for the corresponding segments of an unidentified species of *Ptilomera* from Southern India. Interestingly, the growth slope for the tarsus is steeper than slopes for the other two more proximal segments. This proximo-distal order of increasing growth ratio does not appear to be the case with the other legs, at least not with the hind leg. In *Potamometra berezowskii* the points for the femur and tibia fall on the allomorphic slopes for the corresponding segments in *Ptilomera.* In *Rhyacobates* all three segments fall below the growth slopes for the corresponding segments in the *Ptilomera* species studied, as they do in *Heterobates* and *Potamometropsis.* In *Potamometroides* the points for the femora and tibia fall close to the growth lines for the corresponding segments of the *Ptilomera* species. In *Rheumatogonus* the points for all three segments fall much below the growth lines for the corresponding segments in the *Ptilomera* species from India, and this is probably the most primitive condition in this subfamily.

Halobatinae: In the *Asclepios-Halobates* complex (Halobatini) specific difference in the front leg segments is conspicuous as in the other legs. A rough allomorphic slope for tarsi is steeper than the slopes for the other two segments. Whether this reflects typical growth slopes in the *Asclepios-Halobates* complex or not is not known. Miyamoto (1937), in his study on *Asclepios coreanus miyamotoi,* did not give the data on the development of the front leg.

In *Metrocoris* (fig. 167) the allomorphic slopes for the three segments, except for *M. ståli*(?), conform well to the growth lines for the corresponding segments in *Metrocoris histrio.* In *Eurymetra natalensis* the points for all three segments fall roughly on the allomorphic lines for the corresponding segments in *Metrocoris.* In *Eurymetropsis* and *Eurymetropsiella* the points for the tarsi fall much above the growth line for the same segment in *M. histrio.* In *Ventidius* the allomorphic slope for the tarsi is greater than that for the femur. Whether they reflect the typical growth patterns in *Ventidius* or not is not known, since the front leg in the nymphal specimen was not available for study. In *Esakia kuiterti* the points for the femora and tibia fall above the allomorphic slopes for these segments in *Ventidius.*

Rhagadotarsinae: In *Rheumatobates rileyi palosi* the growth slopes for the three segments from the female third developmental stage to the adult female follow the pattern of proximo-distal gradient of decreasing growth ratio (fig. 168). The points representing the leg segments in other species of the subfamily conform fairly well to the growth lines for the corresponding segments in *R. rileyi palosi.* A conspicuous deviation is noted for the tarsus in the smallest species, *Rheumatobates minutus.* The relatively short tarsus in the largest species, *Rhagadotarsus* (*Caprivia*) *hutchinsoni,* is probably derived from a quite different growth pattern from that of *R. rileyi palosi.*

Trepobatinae: In the postembryonic development of *Trepobates knighti* (fig. 169) the growth ratio for the femur is greater than ratios for the other two segments ($P<0.05$), and the growth lines for the tibia and tarsus are equally steep. The points representing the leg segments in adults of other species of *Trepobates* fall nearly in parallel with the growth lines for the corresponding segments in *T. knighti*. The relatively great distance of the points from the growth lines is presumably due to a rather abrupt increase in growth ratio at the final stage of development, especially for the femora and tibiae. In *Trepobatoides* the point for the tibia is considerably below the growth line for the same segment in *Trepobates*, and the tarsus falls above the growth line for the tarsus. In *Telmatometra*, *Halobatopsis* and *Ovatametra* the points for the femora and tibiae conform well to the growth slopes for the corresponding segments in *Telmatometra indentata*, although *Telmatometra retusa* makes a rather conspicuous deviation. The points for tarsi do not conform well to the growth slope for the same segment in *T. indentata*. In *Metrobates*, while the points for the femora fall rather close to the incomplete growth line for the same segment of *Metrobates porcus*, the allomorphic slopes for the tibiae and tarsi are almost vertical, deviating greatly from the growth lines for the corresponding segments in *M. porcus*. It was further found that the growth slopes for these segments in *M. denticornis*, a larger species, are considerably gentler than the equivalents in *M. porcus*. The deviations of the allomorphic slopes in the more distal segments from the growth slopes for the corresponding segments are thus consistently noted in antennal and all legs in this genus. A rather distinct proximo-distal gradient of decreasing growth ratio among the front tarsal segments appears to exist, as far as the incomplete data indicate. In *Hynesionella* and *Rheumatometra* (female) there appears to be no distinct proximo-distal gradient of decreasing growth ratios, as far as incomplete data indicate.

The tarsal segments

The tarsal segmentation becomes recognizable after the fourth or fifth nymphal stages of development in most genera, although it is distinct in considerably earlier stages in the middle and hind legs of some genera (*e. g., Metrocoris*). In spite of these difficulties in obtaining data, evidence indicates that the growth ratio for the first tarsal segment is greater than that for the second in most genera. There is thus a striking tendency for the first segment to be relatively longer in larger species within the same genus, as will be described below.

(*a*) *The front tarsal segments*

Gerrini: The length of the first tarsal segment relative to the second in *Gigantometra* is 1.22:1. This ratio is greater than the ratio for most species of *Gerris.* In *Gerris* the length of the first relative to the second is definitely greater in the subgenus *Aquarius* (0.67-1.3:1) than in *Gerris s. str.* (0.50-1.0:1), which is shorter in body size. Another subgenus of *Gerris, Limnoporus,* is about as large as *Aquarius* in body size except for G. (*L.*) *canaliculatus,* and the relative length of the first segment to the second ranges from 0.7:1 in the smallest species, G. *(L.) canaliculatus,* to 1.0:1. These ratios are similar to those in *Aquarius,* suggesting that all three subgenera have similar growth relations for these two segments. In *Gerriselloides* the length of the first relative to the second is as in a typical species of *Gerris s. str.*; the same ratio is much smaller in *Gerrisella.* In *Eurygerris,* in spite of relatively short body-size, the length of the first relative to the second is much greater (0.8-1.0:1) than in *Gerris s. str.,* indicating the presence of growth patterns for both segments quite different from those of *Gerris s. str.* In the *Limnogonus s. str.* the length of the first relative to the second segment is 0.5-1.0:1, while it is 0.33-0.60 in *Limnogonellus* which is smaller in body size. This indicates that both subgenera presumably have similar growth patterns for these two segments. In the *Limnometra-Tenagogonus s. str.* complex there is a beautiful series of decrease in the relative length of the first to the second segment from the longer to the shorter species, as will be noted from the table 16. The relative lengths range from 0.84:1 to 1.9:1 in *Limnometra,* from 0.60:1 to 0.90:1 in *Tenagogonus s. str.* which is generally smaller in body size. Both subgenera appear to have similar growth patterns for the tarsal segments. In *Tenagometrella* the length of the first relative to the second segment, as well as the length of the body, are as in typical species of *Limnometra.* In *Tenagometra* and *Tenagogerris* the relative lengths of the first and second segments are as in a typical species of *Tenagogonus s. str.* In *Tachygerris* the first segment is nearly equal to the second in length as in *Eurygerris,* although they are not closely related.

Charmatometrini: The length of the first tarsal segment relative to the second is greatest in *Charmatometra bakeri* which is greatest in body length. In *Brachymetra* there is a clear tendency for the first segment to be relatively longer in the longer species.

Cylindrostethini: In *Cylindrostethus* the relative length of the first to the second segment varies relatively little (0.25-0.55:1), in spite of the fact that the body length varies considerably among species. In a nymph, apparently in the final stage of development, the tarsal segmentation is indistinct. In *Potamobates* the length of the first relative to the second segment also varies relatively little (0.29-0.38:1), in spite of a considerable range in body size among species. This is also the case with *Platygerris* (0.35-0.42:1). In all these genera there is thus no clear tendency for the first segment to be relatively longer in the larger species. In fact, in the last two genera there is evidence that the second segment grows more than, or about as much as, the first segment at the final stage of development (*Potamobates horváthi, Platygerris depressus*), and this tendency in growth pattern is presumably true of *Cylindrostethus.* This peculiar growth pattern is probably the mechanism by which the relatively short first tarsal segment occurs in this tribe.

Eotrechini: In *Eotrechus,* which is largest in body size, the length of the first tarsal segment relative to the second (1:1) is greater than in the other genera of Eotrechini. In *Onychotrechus* the length of the first segment in relation to the second (0.36-0.42:1) is small in comparison with other genera. This has presumably something to do with the presence of the conspicuous and more proximally located claws on the second tarsal segment. There is no conspicuous difference in the relative lengths of the two segments among species in *Amemboa* (0.54-0.75:1). The relative lengths in *Chimarrhometra* are similar to those in *Amemboa.*

Ptilomerinae: The first tarsal segment has apparently been greatly prolonged in evolution of this subfamily. It is always longer than the second segment, often two or three times as long as the second segment. *Rheumatogonus* is the only exception, in which the first segment is shorter than the second segment, and this is presumably the least specialized condition in this subfamily. In an unidentified species of *Ptilomera* from Southern India the first tarsal segment grows much more rapidly than the second at the final stage of development, and this is presumably the underlying mechanism by which the relatively long first tarsal segment is realized in this subfamily. In *Ptilomera* there is a tendency for the length of the first segment relative to the second to be greater in the larger species. That the lengths of the tarsal segments are allometrically derived in this subfamily is also evidenced by the fact that the relative length of the first to the second segment is almost always greater in the females which are longer in body size.

Halobatinae: In the *Asclepios-Halobates* complex (Halobatini) the relative length of the first to the second segment is definitely greater in *Halobates* (0.37-1.15:1), which is longer in body length, than in *Asclepios* (0.15-0.28:1). In Metrocorini the first segment is greatly reduced, often one fourth to one fifth as long as the second segment. The only exception is *Eurymetropsiella,* in which the relative lengths of the first and second segments are as 0.58:1. The front leg tarsal segmentation becomes distinct only in adults of *Metrocoris histrio,* although tarsal segmentation is quite distinct in much earlier stages of development in the middle and hind legs in this species.

Rhagadotarsinae and *Trepobatinae:* In both subfamilies the first tarsal segment is greatly reduced, to about the same degree as in Halobatinae. How this highly reduced first tarsal segment is realized during the development remains to be elucidated.

(b) The middle tarsal segments

Gerrini: The data indicate that the first tarsal segment grows much more than the second segment at the final stage of development in both species of *Gerris* studied (*G. (A.) remigis* and *G. (G.) marginatus*). This difference in growth ratios between the two segments appear to have been inherited in all species of *Gerris.* In *Aquarius* the ratio of the first tarsal segment to the second is 2.9-8.0:1, while the same is 1.7-3.4:1 in *Gerris s. str.,* which is shorter in body length. In another subgenus, *Limnoporus,* the ratio is 4.0-4.8:1 and the body length, except for *G. (L.) canaliculatus,* is as in typical species of *Aquarius.* All these facts indicate that the three subgenera have similar growth patterns in common. In *Gigantometra* the ratio of the first to the second is 9.5:1. Considering the gigantic size of the body in this genus, this extraordinarily long first tarsal segment is easily imaginable, assuming that this genus has similar growth ratios for the tarsal segments to those in *Gerris.* In *Gerriselloides* the ratio of the two segments are as in a typical species of *Gerris s. str.* In *Gerrisella* the relative lengths of the two segments are 3.1-3.3:1. This is much greater than the average ratio in the species of *Gerris s. str.* of equivalent body lengths. In *Eurygerris* the ratio of the first to the second is 4.6-6.0(?):1. This is considerably greater than the ratios in *Gerris s. str.,* although the body length in this genus is shorter than most species of *Gerris s. str.,* indicating the presence of different growth patterns in the two genera.

In the *Limnogonus s. str.-Limnogonellus* complex the ratio of the first to the second is definitely greater in the former than in the latter group which is shorter in body length (3.3-5.4:1, 3.0-4.3:1, respectively). In the *Limnometra-Tenagogonus s. str.* complex there is a tendency, though not highly consistent, for the ratio of the first to the second segment to be greater in the longer species than in the shorter species (3.9-7.0:1, 3.4-4.6:1, respectively). Among the genera related to the *Limnometra-Tenagogonus s. str.* complex, the ratio of the first to the second is relatively great in *Tenagometra* (5.4:1) considering its body length. In *Tenagometrella* the length of the first relative to the second is as in typical species of *Limnometra.* In spite of the difference in absolute lengths of the tarsus between the sexes, the relative lengths of the two segments are about the same in the two sexes, indicating the presence of similar growth ratios with different initial growth indices in different sexes. In *Tenagogerris* the length of the first relative to the second is as in the shorter species of *Limnometra,* or of the longer species of *Tenagogonus s. str.* In *Tachygerris* the length of the first relative to the second ranges from 5.3:1 to 6.0:1; these ratios are similar to those in *Eurygerris.*

Cylindrostethini: In *Cylindrostethus* there is a striking tendency for the ratio of the first to the second to be greater in the longer species; it ranges from 3.1:1 to 6.0:1. In *Potamobates* also there is a striking tendency for the relative lengths of the first to the second to be greater in the longer species (4.0-3.2:1). An exception to this tendency is that the ratio is not greatest in *P. thomasi* which is much longer than the other species. In *Platygerris, P. caeruleus* is much longer than the other two species, but the relative length of the first to the second is smallest (absolute length of the tarsus is greater than the other two species). Unlike that of the front leg, the first segment grows much more rapidly than the second in *Platygerris depressus* and in an unidentified species of *Cylindrostethus* from the Philippines. This growth mechanism is presumably the one by which the relatively long first tarsal segment is realized in the middle leg of this tribe.

Charmatometrini: The ratio of the first to the second segment is greatest in the largest species, *Charmatometra bakeri.* There is a striking tendency in *Brachymetra* for the length of the first relative to the second to be greater in the larger species. In *Eobates* the length of the first in relation to the second is the smallest (3.1-3.2:1) in the tribe, in spite of the fact that the body is longer than in most species of *Brachymetra.* This indicates that for these segments this genus has somewhat different growth patterns from those of the other two genera.

Eotrechini: In *Eotrechus,* according to Esaki (1928), the first tarsal segment is as long as the second. The ratio of the first to the second in *Amemboa* (1.9-2.27:1) is greater than in *Eotrechus,* which is much longer in body length. These two genera are so remotely related that it is hardly conceivable that both genera have similar growth patterns in common. In *Onychotrechus* the first segment is much shorter than the second (0.33-0.44:1). This unique ratio presumably has something to do with the occurrence of the conspicuous claws near the middle of the second tarsal segment. The underlying growth patterns for these two segments are unknown to me, since in an old nymph of *Onychotrechus rhexenor* the tarsal segmentation is not recognizable. In *Chimarrhometra* the length of the first relative to the second is 1.9:1, the ratio close to that of *Amemboa.*

Ptilomerinae: The tarsus is always greatly curved in the dried museum specimens, so that measurements are next to impossible. The first segment is usually five or six times as long as the second.

Halobatinae: In the *Asclepios-Halobates* complex (Halobatini) the length of the first relative to the second segment is greater in *Halobates* (2.7-6.7:1) than in *Asclepios* (2.2-2.3:1) which is shorter in body length. Presumably the greater ratios in *Halobates* are due partly to the presence of a dense mass of hairs of varying degrees of development in various species. The relative lengths of the two segments thus vary considerably at the specific level in *Halobates.* During the postembryonic development of *Metrocoris histrio* the first tarsal segment grows considerably faster than the second. In spite of the considerable difference in body length among species there is no tendency for the first segment to be relatively longer in the longer species, and the ratios of lengths of the two segments range from 8.0:1 to 4.6:1. In *Esakia* the relative lengths are greatest in the female of *E. usingeri* which has the longest body.

Rhagadotarsinae: In the females of this subfamily the ratio of the first to the second segment is greater in *Rheumatobates* than in the two subgenera of *Rhagadotarsus* which are greater in body length. The underlying growth patterns involved remain to be seen.

Trepobatinae: In *Trepobates knighti* the tarsal segmentation is not distinct even at the final nymphal stage. The tendency for the relative length of the first to the second to be greater in the longer species of *Trepobates* is not clear, due primarily to a small range in body size among the species. In *Metrobates* the first segment is shorter than the second; this is unique in the subfamily.

The hind tarsal segments

Gerrini: In *Aquarius* the ratio of the first tarsal segment to the second (1.7-2.8:1) is greater than in *Gerris s. str.* (1.6-2.0:1), which is shorter in body length. In another subgenus, *Limnoporus,* the ratio ranges from 1.9:1 in the shortest species [*G. (L.) canaliculatus*] to 2.6:1. The absolute body length as well as the length of the first tarsal segment relative to the second are as in typical species of *Aquarius.* In the late postembryonic developmental stages the first segment grows much faster than the second segment in the two species of *Gerris* studied. In *Gigantometra* the first tarsal segment is 3.75 times as long as the second, and this is considerably greater than the highest ratio in *Aquarius.* Considering the extraordinarily large body size of this genus, this ratio is conceivable if this genus has similar growth ratios for the two segments to those in *Aquarius.* In *Gerriselloides* the length of the first relative to the second is as in a typical species of *Gerris s. str.* In *Gerrisella* the length of the first relative to the second segment is much smaller (1.1:1) than in any species of *Gerris s. str.* In *Eurygerris* the ratio of the first to the second is as in *Gerris s. str.*

In the *Limnogonus s. str.-Limnogonellus* complex there is no significant difference in the relative length of the first to the second segment between the two genera (1.3-2.4:1, 1.66-2.2:1, respectively). Since the body length in the two subgenera is considerably different, the absence of a difference in the length of the first relative to the second segment denotes the presence of different growth patterns for the two segments in each subgenus. In the *Limnometra-Tenagogonus s. str.* complex there is a striking tendency that the length of the first relative to the second is greater in the longer species (1.8-3.3:1 in *Limnometra,* 1.1-1.8:1 in *Tenagogonus s. str.,* respectively). In *Tenagometra* and *Tenagogerris* the ratio is as in a typical species of *Tenagogonus s. str.* In *Tenagometrella* it is as in a typical species of *Limnometra.* In *Tachy-*

gerris the length of the first relative to the second is as in *Limnogonus* (1.6-2.5:1).

Cylindrostethini: The length of the first tarsal segment relative to the second is greatest in the largest species, *C. productus.* In *C. sumatranus* the ratio of the two segments is quite different from other species of *Cylindrostethus.* The ratio changes from 1.0:1 to 2.0:1 in *Cylindrostethus.* In *Potamobates* the length of the first relative to the second ranges from 1.3:1 to 2.3:1 in the longest species, *P. thomasi.* The relative length is smaller in the shorter species, as will be noted from the table 16. In *Platygerris* the length of the first relative to the second is greatest in the longest species, *P. caeruleus.* Developmental data indicate that the second segment becomes even a little shorter and the first segment grows to be considerably longer at the final stage of development. The above mentioned tendency toward reduction in the length of the first segment relative to the second in the shorter species appears to reflect this growth pattern.

Charmatometrini: The length of the first relative to the second segment is not greatest in the longest species, *Charmatometra bakeri.* In *Brachymetra* there is a tendency for the length of the first relative to the second to be greater in the longer species than in the shorter species. In *Eobates* the ratio, as in the middle leg, is the smallest in the tribe although the body is one of the longest. From the above it seems probable that each genus in this tribe has somewhat different growth patterns for these two segments.

Eotrechini: As in the middle leg the tarsal segments in *Eotrechus,* according to Esaki (1928), are nearly equal in length to each other. In *Amemboa,* which is shorter in body length, the length of the first relative to the second is greater than in *Eotrechus,* but the two genera are not closely related and it cannot possibly be conceived that both genera have, in common, similar growth patterns for these segments. The length of the first relative to the second in *Chimarrhometra,* however, is similar to that in *Amemboa.* In *Onychotrechus* the first segment is much shorter than the second. This unique proportion has presumably something to do with the conspicuous claws located near the middle of the second segment.

Ptilomerinae: In *Ptilomera* and *Potamometra* both tarsal segments are completely fused. In all other genera they are distinct from each other, and the first segment is shorter than or about as long as the second segment. Esaki (1930), however, says that the first segment is about twice as long as the second in *Pleciobates.*

Halobatinae: In *Halobates* the tarsal segments are completely fused. In *Asclepios* they are distinct from each other, and the first segment is shorter than, or about as long as, the second. In the postembryonic development of the hind leg the first segment grows more than the second in *Metrocoris histrio.* In all species of *Metrocoris* studied, however, the first segment is about as long as the second. There is thus no tendency that the first segment is longer in the longer species. In the related genera, *Eurymetra, Eurymetropsis,* and *Eurymetropsiella,* both segments are also nearly equal in length. In *Ventidius* there is a striking tendency for the first segment to be relatively longer in the larger species. The same tendency is seen in *Esakia* though less pronounced.

Rhagadotarsinae: In *Rhagadotarsus* the first segment is as long as, or a little shorter than the second; in *Rheumatobates,* which is shorter in body length, the first segment is considerably shorter than the second in a majority of species.

Trepobatinae: The tarsal segmentation is not distinct even at the fifth nymphal stage in *Trepobates knighti.* There is no great difference in relative lengths of the first and second segments among species of *Trepobates,* probably because the range in body size is rather small in this genus. In *Rheumatometra* and most species of *Metrobatopsis* both segments are completely fused. In many genera the first segment is a little shorter than the second, and this is especially pronounced in *Metrobates* in which the second segment is about two to three times as long as the first. These unique proportions have presumably something to do with the presence of conspicuous claws arising from near the middle of the second segment.

The coxa

The middle coxa: The coxa in the more primitive genera of the Gerridae is shorter than wide. It has apparently become elongate in evolution. In Gerrinae the coxa has apparently been prolonged in *Onychotrechus* and *Amemboa.* In Ptilomerinae the coxa has been greatly prolonged in the female of *Potamometroides.* In all genera of Halobatinae and Trepobatinae the coxa has remained short. In Rhagadotarsinae the coxa has become robust and long in some species of *Rheumatobates.*

The hind coxa: The degree of prolongation of the hind coxa is much more pronounced than in the middle coxa. In Gerrinae the prolongation of the coxa has arisen in *Onychotrechus* and *Amemboa.* In Ptilomerinae it has been apparently prolonged in *Rhyacobates, Potamometra, Heterobates,* and is very conspicuously prolonged in the female of *Potamometroides.* In *Ptilomera* the coxa has remained short, but with a more or less conspicuous spinous process on the caudal margin in the subgenus *Ptilomera s. str.* In Halobatinae the coxa has apparently been prolonged in *Asclepios* and *Halobates.* In Rhagadotarsinae the coxa is wider than long in the subgenus *Capriva* of *Rhagadotarsus;* it is elongate and thickened in various degrees in *Rheumatobates,* which is more specialized.

Phylogenetic changes in relative lengths of the middle and hind legs

In the Gerridae there are only two genera (*Eotrechus* and *Gigantometra*), in which the hind leg is longer than the middle leg. Each genus, as repeatedly pointed out, is structurally very primitive and longest in its tribe. In all other genera the hind leg is shorter than the middle leg. A great contributing factor toward the reduction in length of the hind leg is the reduction of the hind tibia, apparently connected with changes of function of the hind leg [from locomotory organ(?) to steering organ] and with the reduction of the body length in phylogeny. In a great majority of species of Gerridae, except for Trepobatinae, the hind femur is about as long as the middle femur. The hind tarsus is also shorter than the middle tarsus in a great majority of species of Gerridae. It may thus safely be said that the condition in *Gigantometra* and *Eotrechus* is the most primitive, and the hind leg has become shorter in evolution, accompanied mainly by reduction of the tibia and the tarsus.

Shift of position of the claws

The primitive position of the claws is probably the apex of the second tarsal segment in all legs, as seen in *Eotrechus.* From this probable primitive position the claws have shifted their positions more and more basally. In the front leg the claws arise from beyond the middle of the second segment in the majority of genera of Gerrinae and Ptilomerinae. They arise from the middle, or even before the middle, of the second tarsal segment in the great majority of species of Halobatinae and Trepobatinae. Among Rhagadotarsinae the claws arise from the base of a deep cleft of the second segment in the genus *Rhagadotarsus.* In the middle and hind legs the claws are often lost in some genera of Ptilomerinae (*Rhyacobates, Heterobates, Potamometroides*) and Cylindrostethini of Gerrinae (except for *Cylindrostethus* from the Eastern Hemisphere). The claws of the middle leg in Metrocorini and

Trepobatinae are always inconspicuous and arise from near the apex. The claws of the hind leg in Halobatinae and Trepobatinae, however, are relatively well developed and slender, and arise more basally than the claws of the middle leg; sometimes they are conspicuous and located near the middle (*Metrobates*). *Onychotrechus* of Gerrinae is peculiar in that the conspicuous claws arise from near the apical third of the second segment of all tarsi, although the claws are less conspicuous and arise from the apex or near apex in all other genera of the Gerrinae. In *Rhagadotarsus* of Rhagadotarsinae the claws of the both middle and hind legs are inconspicuous, and the claws of the hind leg in *Rheumatobates* are relatively well developed and slender as in Trepobatinae. It is interesting to note that when the conspicuous claws occur on the middle or hind legs, the segment bearing them (second segment) is always unusually long (*Onychotrechus, Metrobates*).

(3) General Discussion

Ontogeny and phylogeny

De Beer (1951) has given an account of various relations between phylogeny and ontogeny. Some of them have bearing upon the present problem. For example, many groups showing phyletic increase in body size exhibit recapitulation; this is, by De Beer's definition, hypermorphosis. In other groups showing phyletic decrease in body size, ontogeny often foreshadows phylogeny.

It has been found in this study that the body has apparently become shorter at all taxonomic levels in the evolution of the great majority of groups of Gerridae. It has also been found that similar allometric growth patterns appear to exist for certain antennal and leg segments within genera and subgenera. When both phenomena occur at the same time, ontogeny, as mentioned above, roughly foreshadows or anticipates phylogeny. The simplified relation of ontogeny to phylogeny in this case is diagrammatically shown in figure 170. In this figure the length of a certain leg or antennal segment in the more primitive and longer species A at its developmental stage B' would roughly be equal to the length of the same segment in the adult of a derived, shorter species B, etc. Rensch (1948) has already discussed the overall tendency towards reduction in body size in evolution of insects in some detail. The case of Gerridae provides generally good support to Rensch's view. If the reduction in body size is a wide spread phenomenon in insects, as Rensch contends and as the present study substantiates, and similar allometric growth mechanisms for certain structures among related species or genera persist generally in insects, the hypothesis diagrammed in figure 170 would generally hold true. It may, therefore, serve as a useful working hypothesis in the study of structural evolution of insects. Of course in the groups showing phyletic increase in body size, as has been observed in a few genera of Gerridae, ontogeny would recapitulate phylogeny if similar allometric growth patterns for certain structures persist among related species.

As already shown, there are many cases of deviation from the above mentioned simple picture. The formation of the consistent secondary allomorphic slope for the hind tibia in many genera of Gerridae is a case in point. Modification of the allomorphic growth pattern, either in growth ratio or initial growth index or both, for the hind tibia has apparently arisen at the specific level in most genera perhaps in adjustment to environmental changes. Many similar cases of alteration of allometric growth ratios in the same phyletic line are known in palaeontology (*e. g.*, Reeve and Murray, evolution of the horse's skull, 1942). Rensch's (1947) studies on contemporaneous vertebrates also indicate that the growth ratios for certain structures shift with enlargement of the body size.

Indeed, the points for the hind tibiae fall roughly on an oblique straight line in many genera of Gerridae, so that there is a consistent tendency for the hind tibia to be relatively shorter in the shorter species of a genus. This fact may easily lead one to suspect that the line (allomorphic line) may reflect the ontogenetic growth line for the hind tibia in the group of species concerned, if ontogenetical evidence is not available. Whatever the underlying growth mechanism may be, the result is a steeper allomorphic slope than the equivalent for the femur in almost all genera of the Gerridae.

As is generally known, the hind leg in the Gerridae is of relatively secondary functional importance. It performs its function as a rudder, or steering organ in water; it is by no means as powerful a locomotory organ in water as the middle leg; on land the hind leg is merely dragged behind when walking and serves as a support to prevent retreat on a slope, as recorded by Miyamoto (1953) for *Metrocoris histrio.* Such being the function there has presumably been selection against powerful and long distal hind leg segments in the evolution of the Gerridae, and more and more relatively short hind leg segments have been favored. If this interpretation is correct the case provides an example of orthoselection, and in this process of selection several different types of alteration in underlying growth patterns are involved.

Taxonomic significance

Taxonomists are agreed that mere body size differences may have no taxonomic significance, since they are often the direct effect of environmental conditions. But greater importance is sometimes attached to differences in proportional size. This tendency is pronounced in works with such groups of insects as Gerridae, in which the appendages and antennae are well developed, and the accounts of them occupy a large part of specific and generic descriptions.

The study of the allometric growth of the antennal and leg segments shows clearly that the proportional lengths of the segments are subject to change depending on different body lengths and the underlying growth patterns for these segments. It is obvious, therefore, that the underlying growth patterns, not the mere proportional lengths of segments in adults, are really of taxonomic importance. The indication obtained in this work in regard to the bearing of different growth patterns upon the taxonomy of Gerridae is not based on much ontogenetical evidence, so that the description of the growth patterns as taxonomic characters in the following lines is tentative. It is my serious intention to correct the mistakes, which will inevitably be made, by studying the development of more forms of the Gerridae in the future. The study of speciation or subspeciation is not the concern here, so that the taxonomic significance of the growth patterns at the levels above the subgenus is discussed below.

At the subfamilial level the Rhagadotarsinae is characterized by the much lower growth ratio for the second antennal segment than for the other segments, and probably by the proximo-distal order of decreasing growth ratios of the hind leg segments. Trepobatinae may be characterized by the relatively low growth ratio and initial growth index for the middle femur. The Ptilomerinae (at least *Ptilomera*) may be characterized by the relatively high initial growth index and the relatively low growth ratio for the proximal segments of the antenna and legs. The proximo-distal increase in growth ratio, which appears to exist at least in the front leg segments in *Ptilomera*, may occur in other genera of Ptilomerinae and thus may characterize this subfamily. In Gerrinae the growth ratio for the femur is probably almost always greater than that for the tibia in the middle leg.

At the tribal level, Cylindrostethini appears to be characterized at least by a smaller growth ratio for the first tarsal segment than for the second in the front leg. Charmatometrini is probably similar in the growth patterns for the leg and antennal segments to the Gerrini.

At the generic or subgeneric level the growth pattern is of even greater taxonomic importance. The following factors were considered in the evaluation of the generic and subgeneric status of groups of Gerridae.

(1) It was *a priori* expected that all congeneric species would have more or less similar growth patterns for the antennal and leg segments, and the points for any segment were expected to fall on or close to the growth lines for the corresponding segments in the representative species of the same genus.

(2) As already observed, however, there is a tendency for certain segments, *e. g.*, the hind tibiae, to form the nearly straight secondary phylogenetic allomorphic lines, due apparently to the differences in growth patterns for these segments at the specific level. In such cases the points for the segments are expected to fall on the same allomorphic line (or slope).

(3) Any striking deviation from (1) or (2) are thought to be probably indicative of marked phylogenetic difference and hence of probable generic or subgeneric rank.

In the three subgenera of *Gerris* the growth patterns for all leg and antennal segments appear to be more or less distinctly different. The growth ratios for at least many antennal and leg segments are probably greater in *Aquarius* than in *Gerris s. str.* *Gerriselloides* has essentially the same growth patterns for all antennal and leg segments as those in *Gerris s. str.*, to which this genus was formerly assigned. *Gerrisella,* which was also formerly included in *Gerris,* presumably has quite different growth patterns for all antennal and leg segments from those of *Gerris.* In *Gigantometra,* which was formerly a part of *Limnometra* but is actually closer to *Gerris,* the growth patterns appear to be significantly different in many segments from those in *Gerris.* In *Tenagogonus* and related genera, *Tenagogerris* and *Tenagometrella,* the growth patterns for at least many antennal and leg segments are presumably similar, although the male in *Tenagometrella* appears to have unusually long initial sizes for all antennal and leg segments. In *Tachygerris* the growth ratios for the first three antennal segments appear to be greater than those in the other genera of Gerrini occurring in the Western Hemisphere. The growth patterns for segments are probably similar in *Limnogonus s. str.* and *Limnogonellus* except that for the fourth antennal segment. *Eurygerris* is apparently characterized by formation of the secondary allomorphic lines for basal leg segments which are more nearly horizontal than in the other genera of Gerrini. Among the genera of Charmatometrini, the most distinctive generic differences appear to be in the proportional lengths of the tarsal segments of the middle and hind legs. The species of *Cylindrostethus* from the Western Hemisphere and those from the Eastern Hemisphere appear to be consistently different in the initial growth indices for all antennal and leg segments. The two groups may be described as distinct genera or subgenera by the future workers, since they differ from each other in some other characters. In *Potamobates* the allomorphic slopes are not continuous with those of *Cylindrostethus* from the Western Hemisphere, suggesting that these genera have significantly different growth patterns for the antennal and leg segments. In *Platygerris* the very long hind and middle femora appear to be realized by the very high growth ratio which apparently characterize this genus.

Among Ptilomerinae, *Rheumatogonus* is characterized by the unique proportional lengths of the antennal and leg segments which must be realized by quite different growth patterns from those of the rest of Ptilomerinae. In Halobatinae the proportional lengths of the front tarsal segments of the *Asclepios-Halobates* complex are presumably realized from a similar growth pattern in all species, although the relative lengths of the middle tibia and the first tarsal segment of the middle leg must be realized by quite different growth patterns at the specific level. In *Metrocoris, Eurymetra, Eurymetropsiella, Eurymetropsis* the growth patterns for the antennal and leg segments are presumably similar. *Ventidius* and *Esakia* are closely related, but the growth patterns at least for the first antennal segment and the middle tibia are presumably significantly different. *Trepobates* and *Telmatometra,* though related, are probably considerably different in the growth patterns at least for the more distal segments of the antenna and legs. *Stenobates* and *Rheumatometroides* are closely related and probably have similar growth patterns for many segments.

The last but by no means the least important thing that this study has revealed is a strong tendency for a species or a group of species, which conspicuously deviates in one segment, to deviate also in all or many other segments. This tendency suggests that for the production of the three legs and antennae, more or less the same physiogenetical system is involved.* If this phenomenon is widely prevalent in the other groups of insects or more widely in other arthropods such as Crustacea, it would be of a considerable practical importance from the viewpoint of taxonomy, since deviations in growth patterns for the other segments would become more or less predictable by the deviation of a single segment. *Potamobates thomasi* Hungerford, *Platygerris caeruleus* Champion, *Cylindrostethus sumatranus* Lundblad, *Limnogonus intermedius* Poisson, etc., are examples. I have noticed deviations in the other structures also at least in a few of these species. Upon more careful study of such structures as the male genitalia and with discovery of related species they may eventually be described as distinct genera or subgenera.

Another tendency to be recalled, in this connection, is that the growth patterns for the proximal segments with higher growth ratios (*e. g.*, the femur, the first antennal segment) often appear to be more similar among related species than those for the more distal segments. This tendency, in turn, indicates that the growth patterns for the first antennal segment and the femur, for instance, are often generically constant. The growth patterns for more distal segments, *e. g.*, for the tarsus and the fourth antennal segment, are often variable at the specific level. Of course the growth patterns for the proximal segments also must differ considerably at the specific level when the segments are more or less greatly modified (*e. g.*, the front femur in *Amemboa* and *Eurygerris*).

(4) Parallelism

Parallelism of structures, which has been observed in the foregoing pages, results from divergence of groups in adjustment to similar environmental factors, combined with genetic potentialities intrinsic to the groups concerned. The apparent cases of parallelism in the Gerridae are summarized below (Table 4).

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* Wigglesworth (1954) suggests a single inductor for the development of legs and antennae in insects in discussing the aristopedia.

TABLE 4.—Table of the cases of parallelism.*

CHARACTERS	NAMES OF GROUPS
1. Reduction in length of third relative to fourth rostral segment.	Eotrechini (Gerrinae), Cylindrostethini (Gerrinae), Charmatometrini (Gerrinae), and *Ventidius-Esakia* complex (Halobatinae).
2. Reduction in length of second relative to third antennal segment in more specialized shorter forms.	*Aquarius*, *Gerris s. str.* (Gerrini, Gerrinae), *Limnogonus s. str.-Limnogonellus* complex (Gerrini, Gerrinae), and *Ventidius-Esakia* complex (Halobatinae).
3. Reduction of pronotum in wingless forms.	*Limnogonus s. str.-Limnogonellus* complex, *Limnometra-Tenagogonus s. str.* complex, and *Eurygerris* (Gerrini, Gerrinae).
4. Shift of position of abdominal spiracles caudad in more specialized shorter species.	*Aquarius*, *Gerris s. str.*, and *Limnometra-Tenagogonus s. str.* complex (Gerrini, Gerrinae); *Cylindrostethus-Potamobates* series (Cylindrostethini, Gerrinae), Charmatometrini (Gerrinae), and Rhagadotarsinae.
5. Reduction of connexival spine in more specialized and shorter forms.	Gerrini (Gerrinae), and Cylindrostethini (Gerrinae).
6. Production of secondary connexival spine.	Ptilomerinae except *Ptilomera* (*Proptilomera*), *Rheumatogonus*, and *Potamometropsis; Eurygerris* and *Tenagogonus* (Gerrini, Gerrinae), and *Trepobates* (Trepobatinae).
7. Median emargination of ventral apical margin of seventh abdominal segment in males of more specialized forms.	*Aquarius*, and *Gerris s. str.* (Gerrini, Gerrinae); Cylindrostethini (Gerrinae).
8. Ventral apical margin of seventh abdominal segment in female lobately produced.	*Tachygerris* (Gerrini, Gerrinae), *Platygerris* (Cylindrostethini, Gerrinae), *Metrocoris* (Halobatinae), *Rheumatometroides* and *Metrobatopsis* (Trepobatinae).
9. Ventral basal area of eighth abdominal segment depressed.	*Rhyacobates* and *Ptilomera* (Ptilomerinae); *Potamobates* and *Platygerris* (Cylindrostethini, Gerrinae).
10. Formation of median longitudinal ridge in eighth abdominal segments in males.	*Heterobates* and *Rhyacobates* (Ptilomerinae); *Aquarius* and *Gerris s. str.* (Gerrini, Gerrinae).
11. Modification of apical margin of eighth abdominal segments in males.	Cylindrostethini (Gerrinae), and Halobatini (Halobatinae).
12. Rotation of pygophore.	*Potamobates* and *Platygerris* (Cylindrostethini, Gerrinae); *Halobates* (Halobatinae), and *Metrobatopsis* (Trepobatinae).

TABLE 4.—Table of the cases of parallelism—*Continued*

CHARACTERS	NAMES OF GROUPS
13. Modification of apical margin of pygophore.	*Amemboa* and *Chimarrhometra* (Eotrechini, Gerrinae); *Metrocoris* and *Eurymetropsis* (Halobatinae).
14. Modification of front femur.	Conspicuously in *Eurygerris* and *Amemboa* (Gerrini, Gerrinae); less conspicuously in *Metrocoris* and *Ventidius* (*Ventidioides*) (Halobatinae), and *Ptilomera* (Ptilomerinae).
15. Prolongation of middle and hind coxae.	*Onychotrechus* and *Amemboa* (Eotrechini, Gerrinae); *Eurygerris* (Gerrini, Gerrinae); *Potamometroides*, *Rhyacobates* and *Heterobates* (Ptilomerinae); Rhagadotarsinae.
16. Reduction of hind tibia.	All groups except *Trepobates* (Trepobatinae) and Rhagadotarsinae.
17. Prolongation of femora of all legs and first antennal segment.	*Platygerris* (Cylindrostethini, Gerrinae) and Ptilomerinae except for *Rheumatogonus*.
18. Fusion of hind tarsal segments.	*Ptilomera* and *Potamometra* (Ptilomerinae); *Halobates* (Halobatinae); *Rheumatometra* and *Metrobatopsis* (Trepobatinae).
19. Loss of claws.	Western Hemisphere *Cylindrostethus* (Gerrinae); *Heterobates*, *Rhyacobates*, and *Potamometroides* (Ptilomerinae).
20. More distal separation of R+M into R and M in specialized genera.	Gerrini (Gerrinae), Cylindrostethini (Gerrinae) and Eotrechini (Gerrinae).
21. Concomittal prolongation of apical abdominal segments with reduction of preceding segments.	All groups. Very conspicuously in *Cylindrostethus-Potamobates-Platygerris* series (Cylindrostethini, Gerrinae), *Limnometra-Tenagogonus s. str.* complex and *Amemboa* (Gerrini, Gerrinae), *Asclepios-Halobates* complex (Halobatinae), and *Proptilomera-Ptilomera* complex (Ptilomerinae).
22. Loss of indentation of eyes.	*Amemboa* (Eotrechini, Gerrinae), *Platygerris* (Cylindrostethini, Gerrinae).
23. Modification of suranal plate on lateral margin.	*Amemboa* (Eotrechini, Gerrinae), *Gerrisella* (Gerrini, Gerrinae), Cylindrostethini (Gerrinae), *Ptilomera s. str.* (Ptilomerinae), *Metrobatopsis*, *Hynesionella*, *Rheumatometroides* and *Stenobates* (Trepobatinae).
24. Loss of parameres.	All subfamilies except for Ptilomerinae.
25. Mutual functional replacement between parameres and lateral projection of suranal plate.	*Amemboa* (Eotrechini, Gerrinae), *Gerrisella* (Gerrini, Gerrinae), *Metrobatopsis* and *Hynesionella* (Trepobatinae).

TABLE 4.—Table of the cases of parallelism—*Concluded*

CHARACTERS	NAMES OF GROUPS
26. Metacetabular suture reaching or nearly reaching anterolateral angle of first abdominal tergite.	Ptilomerinae and Halobatinae.
27. Metacetabular suture connected with posterior margin of metathoracic postnotum in wingless forms.	Rhagadotarsinae and Trepobatinae.
28. Lateral loss of primary intersegmental suture between mesonotum and metanotum.	Some genera of Gerrinae, Halobatinae, Trepobatinae and Rhagadotarsinae.

* The cases, in which certain primitive structures are retained only in certain genera of primitive subfamilies and are lost completely in all other more specialized (but not necessarily directly derived) subfamilies, are not enumerated.

TABLE 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters.

	PRIMITIVE	SPECIALIZED
1	Freshwater habitat.	Marine habitat.
2	Body long and slender (in most cases).	Body short and wide (in most cases).
3A	Ventral surface of body without modication in female.	Ventral surface of body medially with a well defined area extending from mesosternum to apical abdominal segments in female.
3B	Body surface smooth.	Body clothed with velvety hairs.
4	Anterior margin of head produced medially (clypeal region) and directed forward.	Anterior margin of head rounded and bent ventrally.
5*	Antenniferous tubercles well developed.	Antenniferous tubercles greatly reduced.
6	Rostrum free from ventral surface of body when at rest.	Rostrum on ventral surface of body when at rest.
7*	Rostrum slender.	Rostrum incrassate.
8*	Antennal cavity open anteriorly and dorsally.	Antennal cavity open more posteriorly and more ventrally.
9	Basal margin of clypeus distinct.	Basal margin of clypeus lost.
10	Anterior margin of clypeus in contact with labrum.	Anterior margin of clypeus separated from labrum by a membranous area.
11	Mandibular and maxillary plates separated from each other.	Mandibular and maxillary plates fused together.
12*	Bucculae formed.	Bucculae not formed.
13*	Eyes globular in shape and small.	Eyes elongate and large.
14*	Eyes with indentation.	Eyes without indentation.
15A	Eyes not covering anterolateral angles of pronotum.	Eyes covering anterolateral angles of pronotum.
15B	Eyes not completely covering lateral margins of pronotum.	Eyes completely covering lateral margins of pronotum.
16	Antennal segments subequal in length to each other.	Antennal segments not subequal to each other.
17	First antennal segment shorter than or equal to second and third segments together.	First antennal segment longer than two following segments together.
18	First antennal segment shorter than three following segments together.	First antennal segment longer than three following segments together.
19	First antennal segment not incrassate in male.	First antennal segment strongly incrassate in male.
20	Relative lengths of first and second antennal segments without sexual difference.	Relative lengths of first and second antennal segments sexually different.
21A	Third antennal segment not modified in male.	Third antennal segment modified in male.
21B	Third antennal segment with simple basal accessory segment.	Third antennal segment with ear-shaped basal accessory segment.
22A	Relative lengths of second and third antennal segments without significant sexual difference.	Relative lengths of second and third segments sexually different.
22B	Second and third antennal segments not modified.	Second and third antennal segments modified distally.
23	Fourth antennal segment straight.	Fourth antennal segment curved.
24*	Pronotum prolonged in wingless form.	Pronotum not prolonged in wingless form.

TABLE 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters—*Continued*

	PRIMITIVE	SPECIALIZED
25	Pronotum simply rounded on apical margin in wingless form.	Pronotum greatly modified apically.
26	Lateral longitudinal suture of mesothorax separating mesonotum from mesopleuron present.	Lateral longitudinal suture of mesothorax separating mesonotum from mesopleuron lost.
27	Longitudinal suture separating mesosternum from mesopleuron present.	Longitudinal suture separating mesosternum from mesopleuron lost.
28	Mesosternum without median longitudinal sulcus anteriorly.	Mesosternum with median longitudinal sulcus anteriorly.
29	Anterior margin of mesosternum simply rounded.	Anterior margin of mesosternum more or less greatly produced medially.
30	Mesonotum without depressions near anterior margin.	Mesonotum with well marked paired depressions near anterior margin.
31	Mesonotum without conspicuous median longitudinal impression.	Mesonotum with a very conspicuous median longitudinal impression.
32A	Intersegmental suture between meso- and metanota retained dorsally.	Intersegmental suture between meso- and metanota lost dorsally.
32B	Intersegmental suture between meso- and metanota dorsally not carinate.	Intersegmental suture between meso- and metanota carinate dorsally.
33	Intersegmental suture between meso- and metanota retained laterally.	Intersegmental suture between meso- and metanota lost laterally.
34A	Metacetabular suture poorly developed dorsally.	Metacetabular suture connected with primary intersegmental suture dorsally.
34B	Metacetabular suture poorly developed dorsally.	Metacetabular suture connected with anterolateral angle of first tergite.
35	Metanotum without lateral longitudinal elevation.	Metanotum with well developed lateral longitudinal elevation.
36	Metacetabulum simple on posterolateral angle.	Metacetabulum flattened and broad posterolaterally, and often acute at tip.
37	Metacetabulum simple on posterolateral angle in female.	Metacetabulum with a conspicuous apical process in female.
38	Elevated metacetabular regions nearly parallel-sided.	Elevated metacetabular regions strongly convergent anteriorly.
39A	Metasternum relatively long.	Metasternum short.
39B	Metasternum relatively short, not greatly produced aneriorly.	Metasternum relatively short, and greatly produced anteriorly.
40	Metasternum represented by a narrow plate reaching metacetabular region.	Metasternum represented merely by a small median subtriangular plate.
41	Omphalium present.	Omphalium absent.
42	Omphalial groove present.	Omphalial groove absent.
43*	Metathoracic spiracle oriented nearly cephalo-caudally.	Metathoracic spiracle oriented nearly dorsoventrally.
44	Abdomen normally exposed in female.	Abdomen withdrawn into thoracic cavity in female.
45A	Pregenital abdominal segments more or less uniform and long.	Pregenital abdominal segments not uniform and short.
45B	Pregenital segments without depression centrally in male.	Pregenital segments with a depression in male.
46*	Abdominal spiracles placed anterior to middle of each segment.	Abdominal spiracles placed at middle of each segment.

TABLE 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters—*Continued*

	PRIMITIVE	SPECIALIZED
47	First abdominal segment well retained ventrally.	First abdominal segment completely lost ventrally.
48	Anterior margin of first tergite nearly straight.	Anterior margin of first tergite flattened W-shaped.
49	Anterior margin of first tergite retained.	Anterior margin of first tergite lost.
50	Anterior margin of first tergite without modification in female.	Anterior margin of first tergite with a process, elevation, etc. in female.
51	First connexival segment well defined posteriorly.	First connexival segment with posterior margin lost.
52	Ventrolateral longitudinal suture of pregenital abdominal segments present.	Ventrolateral longitudinal suture of pregenital segments absent.
53	Connexivum more or less horizontal or slightly reflexed in female.	Connexivum greatly reflexed and folded onto dorsum in female.
54	Anterior margin of second tergite retained.	Anterior margin of second tergite lost at least medially.
55	Second and third connexival segments not fused.	Second and third connexival segments fused.
56	Anterior margin of third tergite retained.	Anterior margin of third tergite lost.
57	Sixth tergite not modified in female.	Sixth tergite with more or less conspicuous modification (round elevation, etc.) in female.
58	Seventh abdominal segment shorter than sixth on ventral longitudinal axis.	Seventh abdominal segment longer than sixth on ventral median longitudinal axis.
59*	Connexival spine conspicuous, especially in female (in some groups).	Connexival spine absent (in some groups).
60	Posterolateral angle of seventh abdominal segment simple in female.	Posterolateral angle of seventh abdominal segment conspicuously modified (spinous process, lateral projection etc.) in female.
61A	Ventral apical margin of seventh abdominal segment not modified in male.	Ventral apical margin of seventh abdominal segment greatly modified in male.
61B	Ventral apical margin of seventh abdominal segment simply concave in male.	Ventral apical margin of seventh abdominal segment with a median emargination in male.
61C	Ventral apical margin of seventh abdominal segment simply concave in male.	Ventral apical margin of seventh abdominal segment with conspicuous paired processes in male.
61D	Ventral apical margin and surface of seventh abdominal segment unmodified in male.	Ventral surface of seventh abdominal segment modified (depression etc.) in male.
62A	Ventral apical margin of seventh abdominal segment simply concave or nearly horizontal in female.	Ventral apical margin of seventh abdominal segment with large lobate projection in female.
62B	Ventral basal margin of seventh abdominal segment not strongly produced anteriorly in female.	Ventral basal margin of seventh abdominal segment strongly produced anteriorly in female.
63A	Eighth abdominal segment not prolonged in male.	Eighth abdominal segment greatly prolonged in male.
63B	Eighth abdominal segment not modified besides prolongation in male.	Eighth abdominal segment greatly modified besides prolongation in male.
64A	Ventral surface of eighth abdominal segment smooth in male.	Ventral surface of eighth abdominal segment depressed basally in male.
64B	Ventral surface of eighth abdominal segment smooth in male.	Ventral surface of eighth abdominal segment with a median longitudinal ridge in male.

TABLE 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters.—*Continued.*

	PRIMITIVE	SPECIALIZED
64C	Ventral surface of eighth abdominal segment smooth in male.	Ventral surface of eighth segment with round elevated areas or with apical depression in male.
65	Ventral apical margin of eighth abdominal segment not symmetrical in male.	Ventral apical margin of eighth abdominal segment asymmetrical in male.
66A	Basal lateral process on ninth tergite small and inconspicuous in male.	Basal lateral process on ninth tergite symmetrically greatly developed in male.
66B	Basal lateral process on ninth tergite small and inconspicuous in male.	Basal lateral process of ninth tergite greatly asymmetrically developed in male.
67	Basal region of ninth tergite without internal hook.	Basal region of ninth tergite with internal hook.
68A	Ninth tergite simple in male.	Ninth tergite greatly modified on basal lateral margin.
68B	Ninth tergite simple in male.	Ninth tergite greatly dilated at or beyond middle in male.
69A	Parameres present and simple.	Parameres lost, or greatly reduced.
69B	Parameres simple.	Parameres greatly modified (enlarged, with shaggy hairs apically etc.)
70	Parameres symmetrical.	Parameres asymmetrical.
71	Pygophore not prolonged.	Pygophore greatly prolonged.
72A	Pygophore not rotated.	Pygophore rotated on transverse axis.
72B	Pygophore not rotated.	Pygophore rotated on vertical axis.
73	Pygophore without conspicuous projection on lateral margin.	Pygophore with conspicuous modification on lateral margin (process, mass of shaggy hairs, etc.).
74	Pygophore simply rounded on apical margin.	Pygophore bifurcate or curiously modified on apical margin.
75A	Pygophore without modification on ventral surface.	Pygophore with a median longitudinal elevation.
75B	Pygophore without modification on ventral surface.	Pygophore with a process on median longitudinal axis.
76	Styloide present.	Styloide lost.
77	Apical, dorsal, basal and ventral plates of endosoma incompletely fused, not forming a ring.	Apical, dorsal, basal and ventral plates of endosoma completely fused to form a ring.
78	Apical plate of endosoma clearly separated from dorsal plate.	Apical plate of endosoma fused with dorsal plate.
79	Ventral plate of endosoma distinctly paired and membranous.	Ventral plates of endosoma largly fused and sclerotized.
80	Basal plate of endosoma separated from ventral plate or from dorsal plate.	Basal plate of endosoma fused either with ventral plate or with dorsal plate or with both.
81	Apical plate of endosoma present.	Apical plate of endosoma lost.
82	Apical segment of endosoma simply rounded apically.	Apical segment of endosoma prolonged and modified apically.
83	Third valvulae present.	Third valvulae lost.
84	Rami of first valvulae distinguishable from process of ninth tergite.	Rami of first valvulae indistinguishably fused to process of ninth tergite.
85	Apical margin of intervalvular membrane not sclerotized.	Apical margin of intervalvular membrane highly sclerotized.

TABLE 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters—*Continued*

	PRIMITIVE	SPECIALIZED
86	Valvulae normally developed.	Valvulae greatly reduced.
87	Winged.	Wingless.
88	Embolium is not formed.	Embolium is formed.
89	Basal part of forewing membranous.	Basal part of forewing coriaceous.
90	Coriaceous region of forewing occupies basal half.	Coriaceous region of forewing occupies basal one fourth to one third.
91	R+M and Cu arise independently from near base of forewing.	R+M and Cu basally fused.
92	Sc_2 united with R+M at point of separation of the latter into R and M.	Sc_2 united with R+M at the point basal to point of separation of the latter into R and M.
93	Sc_2 present.	Sc_2 lost.
94	R+M branches into R and M apically.	R+M not branching into R and M apically.
95	Cu and A joined apically.	Cu and A not joined apically.
96	Line of weakness on forewing absent.	Line of weakness on forewing present.
97	Hind leg longer than middle leg.	Hind leg shorter than middle leg.
98	Front trochanter without a tubercle.	Front trochanter with a tubercle.
99	Claws arise from apex of second tarsal segment of front leg.	Claws arise from near middle of second tarsal segment of front leg.
100	Front trochanter without a tubercle.	Front trochanter with a tubercle.
101	Front femur not modified in male.	Front femur greatly modified (dilated, strongly curved, with tubercle etc.) in male.
102	Front tibia without apical conspicuous process.	Front tibia with conspicuous apical process.
103A	Front tibia without denticles on inner margin.	Front tibia with a series of denticles on inner margin.
103B	Front tibia without tuberculous process on inner margin in male.	Front tibia with tuberculous process on inner margin in male.
104	Apical region of femur and basal region of tibia of front leg without conspicuous tubercles.	Apical region of femur and basal region of tibia of front leg with conspicuous tubercles.
105	First tarsal segment of front leg long.	First tarsal segment of front leg greatly reduced.
106	Middle femur lacks a fringe of long hairs.	Middle femur provided with a fringe of long hairs.
107	Middle tibia lacks a row of long hairs on inner margin.	Middle tibia bears a row of long hairs on inner margin.
108	Middle tarsus has claws.	Middle tarsus without claws.
109	Middle first tarsal segment without a row of long hairs.	Middle first tarsal segment with a row of long hairs.
110	Middle tibia and hind femur as long as or shorter than length of body.	Middle tibia and hind femur considerably longer than length of body.
111A	Claws arise apically or from near apex of second tarsal segment in middle and hind legs.	Claws arise from near middle of second tarsal segment in middle and hind legs.
111B	Claws present in middle leg.	Claws absent in middle leg.
112	Hind coxa wide : than or as wide as long.	Hind coxa longer than wide.

TABLE 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters—*Concluded*

	PRIMITIVE	SPECIALIZED
113	Hind coxa without spinous process on apical margin.	Hind coxa with a spinous process on apical margin.
114	Hind first and second tarsal segments not fused.	Hind first and second tarsal segments fused.
115	Hind tarsal claws normal in size.	Hind tarsal claws conspicuous in size.
116	Hind tarsal claws present.	Hind tarsal claws lost.

* Primitive or specialized alternative is based on association. See p. 47.

Characters Whose Primitive or Specialized Alternatives Were Not Determined.

	O	X
117	Pronotum with yellow median longitudinal and marginal stripes.	Pronotum with median and marginal black stripes.
118**	Dorsal surface without median longitudinal sulcus.	Dorsal surface of head with a median longitudinal sulcus.
119**	Mesonotum with an inconspicuous median longitudinal impression.	Mesonotum without a median longitudinal impression.
120**	Metanotum with a median longitudinal sulcus.	Metanotum without a median longitudinal sulcus.
121	Metathoracic spiracle located at some distance from pronotum in wingless forms.	Metathoracic spiracle located very close to lateral margin of pronotum in wingless forms.
122	Ovipositor formed.	Ovipositor not formed.
123	Middle femur longer than middle tibia.	Middle femur shorter than middle tibia.

** Nymphal characters.

124†	Relative lengths of mesosternum and metasternum.
125	Relative lengths of first and second tarsal segment of front leg.
126	Relative lengths of tibia and femur of middle leg.
127	Relative lengths of first and second tarsal segments of middle leg.
128	Relative lengths of tibia and femur of hind leg.
129	Relative lengths of first and second tarsal segments of hind leg.

† The smaller the length of mesosternum relative to metasternum, the more primitive.

CLASSIFICATION

Earlier Classifications

It seems worth-while to review some previous works that have contributed to the current concept of the classification of the Gerridae before discussing a new interpretation. Dufour (1834) included the Hydrometridae, Veliidae and Gerridae within the family Amphibicorises based primarily on the habitat. Amyot and Serville (1843) and other workers in the nineteenth century treated the Gerridae as a tribe or subfamily (group by Amyot and Serville, 1843) of the Amphibicorises of Dufour, or of the Gerridae *s. lat.* Bianchi (1896) subdivided the family Gerridae into two subfamilies based on the ratio of the length of the body to the width. His division is as follows:

1. Subfamily Halobatinae, with the genera *Halobates* Eschscholtz, 1822, *Halobatopsis* Bianchi, 1896, *Trepobates* Uhler, 1894, *Chimarrhometra* Bianchi, 1896, *Brachymetra* Mayr, 1865, *Metrocoris,* Mayr, 1865, *Rheumatobates* Bergroth, 1892, *Hymenobates* Uhler, 1894, *Metrobates* Uhler, 1871, *Platygerris,* B.-White, 1883, *Potamometra* Bianchi, 1896.

2. Subfamily Gerrinae

A. Gerrids, with the genera *Hydrobates* Erichson, 1848 (*Cylindrostethus* Fieber, 1861), *Gerris* Fabricius, 1794, *Limnotrechus* Stål, *Hygrotrechus* Stål, *Limnoporus* Stål, 1868, *Limnogonus* Stål, 1868 (*Lamprotrechus* Reuter, 1883), *Limnometra* Mayr, 1865, *Tenagogonus* Stål, 1853.

B. Ptilomerae, with genera *Ptilomera* Amyot et Serville, 1843, and *Heterobates* Bianchi, 1896.

Bergroth (1908) employed the shape of eyes for the recognition of the two subfamilies (tribes), *i. e.,* those genera with indented eyes belong to the Gerrinae and those without indentation are the Halobatinae. This character has been used widely until the present time. Meanwhile, Esaki (1929) raised Bianchi's Ptilomerae to the subfamily rank with *Rheumatogonus, Ptilomera, Potamometra, Rhyacobates, Teratobates, Heterobates* as members. Another significant contribution of Esaki (1928c) was his establishment of synonymy for invalid genera of Distant. Esaki (1928a) further maintains that the Haloveliinae should be included within the Gerridae on the basis of the four-jointed rostrum, the unusually long distance between the bases of the anterior and posterior legs, and the long posterior femur which extends beyond the end of the abdomen, and included *Strongylovelia, Xenobates, Halovelia,* and

Entomovelia within the Haloveliinae. The Haloveliinae was later transferred to the Veliidae by China and Usinger (1949), and further raised to the familial rank by Poisson (1956). Lundblad (1933) established the subfamily Rhagadotarsinae for the genus *Rhagadotarsus* on the basis of some good morphological characters, such as the well-developed genae, the absence of the accessory segment in the third antennal segment, the mesonotum and metanotum being laterally well defined by a longitudinal line, etc. Meanwhile, the Hermatobatinae was established by Coutière and Martin (1901) for the genus *Hermatobates.* Since then this subfamily has been treated as a part of the Gerridae in various works including the recent monographic work on this group by China (1957). According to Kenaga (1941) and Kuitert (1942) who last worked out the key to genera of the Gerridae of the world, the breakdown of genera of the Gerridae is as follows:

The Gerrinae.—*Onychotrechus* Kirkaldy, *Cylindrostethus* Fieber, *Rheumatotrechus* Kirkaldy, *Potamobates* Champion, *Limnogonus* Stål, *Eotrechus* Kirkaldy, *Gerris* Fabricius, *Tenagogonus* Stål, *Potamometropsis* Lundblad.

The Ptilomerinae.—*Rheumatogonus* Kirkaldy, *Ptilomera* Amyot et Serville, *Potamometra* Bianchi, *Heterobates* Bianchi, *Esakobates* Lundblad, *Pleciobates* Esaki, *Rhyacobates* Esaki, *Teratobates* Esaki.

The Halobatinae.—*Amemboa* Esaki, *Platygerris* B. White, *Charmatometra* Kirkaldy, *Brachymetra* Mayr, *Metrocoris* Mayr, *Eurymetra* Esaki, *Ventidius* Esaki, *Esakia* Lundblad, *Halobates* Eschscholtz, *Asclepios* Distant, *Trepobates* Uhler, *Metrobates* Uhler, *Telmatometra* Bergroth, *Cryptobates* Esaki, *Metrobatopsis* Esaki, *Rheumatometra* Kirkaldy, *Halobatopsis* Bianchi, *Naboandelus* Distant, *Rheumatobates* Bergroth.

The Hermatobatinae.—*Hermatobates* Coutière et Martin.

After Kenaga and Kuitert, China (1943) described *Hynesia.* Hungerford (1954) reduced *Hynesia* to a subgenus of *Rheumatobates,* and transferred *Rheumatobates* to Rhagadotarsinae. Hungerford (1951) also described *Potamometroides* from Madagascar. Poisson described *Gerrisella* (1940) as a subgenus of *Gerris.* He also described *Tenagometra* and *Tenagogonellus* (1948) as subgenera of *Tenagogonus, Eurymetropsis* (1948), *Hynesionella* (1949), *Eurymetropsiella* (1950), *Eurymetropsielloides* (1956), and *Tenagometrella* (1957) as independent genera and subgenus. Drake (1957 described *Tachygerris* for the groups of species of *Tenagogonus* from the Western Hemisphere. In their recent studies (1958-1959) Hungerford and Matsuda have described *Gigantometra, Eurygerris, Tenagogerris, Gerriselloides, Rheumatometroides, Trepobatoides* as new genera, *Limnogonellus, Ventidioides, Proptilomera* as new subgenera, raised *Gerrisella* to the generic rank, and reduced *Teratobates* and *Esakobates* to the synonyms of *Heterobates* and *Rhyacobates* respectively.

A New Classification

As Matsuda (1957) pointed out, and more detailed morphological and evolutionary studies of structures in the foregoing sections of this work have verified, the primary characters in the subfamily classification of the Gerridae thus far used, such as the shape of eyes, and the length of the body relative to width, are by no means well stabilized at the level of higher taxonomic units. One of the most important higher taxonomic characters appears to be the intersegmental suture between the mesonotum and metanotum. The morphological origin of this suture (either primary or secondary definitive) varies in various groups of Gerridae, indicating various stages of evolution. Correlated with this the forewing venation was found to be fairly well stabilized within each group, indicating also various stages of evolution. In addition to these fundamental characters the following five characters were found to be significant diagnostic features in separating the subfamilies. So altogether seven characters are used in describing each subfamily. The five additional characters are 12, 27, 41, 47, and 122 on table 5.

SUBFAMILY GERRINAE AMYOT AND SERVILLE

Forewing with veins R + M connected with Sc by Sc_2; R + M and Cu fused basally. Primary intersegmental suture between mesonotum and metanotum either distinct or obliterated laterally. Lateral longitudinal suture separating mesonotum and mesopleuron absent in most genera. Genae not lobately developed. Omphalium always present. First abdominal segment ventrally lost. Well formed ovipositor absent.

In the Gerrinae the characters 23, 24, 33, 34A, 42, 48, 59, 105 are diagnostic characters separating the four tribes.

(*a*) Tribe GERRINI Amyot and Serville

Fourth antennal segment straight and slender. Pronotum in wingless forms fully developed in most species. Intersegmental suture between meso- and metanota obliterated laterally in some genera. Metacetabular suture never united with posterior margin of mesonotum. Omphalial groove absent in most genera. Anterior margin of first abdominal tergite flattened W-shaped. Connexival spine present in many species. First front tarsal segment not reduced.

The following genera belong to this tribe:

Gerris Fabricius including three subgenera (*Gerris* Fabricius *s. str.*, *Aquarius* Schellenberg, *Limnoporus Stål*), *Gigantometra* Hungerford and Matsuda, *Gerriselloides* Hungerford and Matsuda, *Gerrisella* Poisson, *Tenagometrella* Poisson, *Tenagogerris* Hungerford and Matsuda, *Limnogonus* Stål including *Limnogonus* Stål *s. str.* and *Limnogonellus* Hungerford and Matsuda, *Tachygerris* Drake, *Tenagogonus* Stål including three subgenera (*Tenagogonus* Stål *s. str.*, *Limnometra* Mayr, *Tenagometra* Poisson).

(*b*) CYLINDROSTETHINI Matsuda, new tribe

Fourth antennal segment short and curved, Pronotum in wingless forms never prolonged. Intersegmental suture between meso- and metanota distinct laterally. Metacetabular suture dorsally connected with intersegmental suture. Omphalial groove present except for *Platygerris.* Anterior margin of first abdominal tergite flattened W-shaped. Connexival spine present in most species. First front tarsal segment greatly reduced.

The following genera belong to this tribe:

Cylindrostethus Fieber, *Potamobates* Champion, *Platygerris* Buchanan-White.

(*c*) CHARMATOMETRINI Matsuda, new tribe

Fourth antennal segment always straight. Pronotum in wingless forms fully prolonged. Intersegmental suture between meso- and metanota distinct or obliterated laterally. Metacetabular suture not connected with intersegmental suture. Omphalial groove present. Anterior margin of first abdominal tergite nearly straight. Connexival spine absent. First front tarsal segment not reduced.

The following genera belong to this tribe:

Charmatometra Kirkaldy, *Eobates* Drake and Harris, *Brachymetra* Mayr.

(*d*) EOTRECHINI Matsuda, new tribe

Fourth antennal segment straight. Pronotum in wingless forms not prolonged. Intersegmental suture between meso- and metanota distinct laterally except for *Amemboa.* Metacetabular suture not reaching posterior margin of mesonotum. Omphalial groove absent. Anterior margin of first abdominal tergite flattened W-shaped. Connexival spine absent. First front tarsal segment not reduced.

The following genera belong to this tribe:

Eotrechus Kirkaldy, *Onychotrechus* Kirkaldy, *Amemboa* Esaki, *Chimarrhometra* Bianchi, *Rheumatotrechus* Kirkaldy(?).

SUBFAMILY PTILOMERINAE BIANCHI

Forewing with veins R + M and Cu basally either distinct or fused. Sc not connected to R + M by an oblique vein. Primary intersegmental suture always distinct laterally. *Metacetabular suture dorsally connected with anterolateral angle of first abdominal tergite.* Lateral longitudinal suture separating mesonotum from mesopleuron absent in most genera (present only in *Potamometra*). Genae not lobately developed. Omphalium present. First abdominal segment ventrally absent. Ovipositor not formed.

The following genera belong to this subfamily:

Ptilomera Amyot and Serville including two subgenera (*Ptilomera* Amyot and Serville *s. str.*, *Proptilomera* Hungerford and Matsuda), *Potamometra* Bianchi, *Rheumatogonus* Kirkaldy, *Potamometropsis* Lundblad, *Potamometroides* Hungerford, *Hetrobates* Bianchi, *Rhyacobates* Esaki, *Pleciobates* Esaki.

SUBFAMILY HALOBATINE BIANCHI

Forewing with R + M and Cu veins fused basally. R + M + Cu branched into R + M and posterior Cu veins respectively. R + M either connected or not connected with embolium by an oblique vein. Cu joined with vein A apically. Definitive intersegmental suture dorsally represented by posterior margin of mesothoracic scutoscutellum, obliterated laterally in most genera. Lateral longitudinal suture separating mesonotum from mesopleuron absent. Genae not lobately developed. Omphalium present. First abdominal segment absent ventrally. Ovipositor not formed.

The two tribes belonging to this subfamily can be divided by characters 1, 3B, 9, 87, 107, 109, 113.

(*a*) Tribe HALOBATINI Bianchi

Marine habitat. Body surface clothed with short velvety hairs. Clypeus with basal margin distinct. Middle tibia and first middle tarsal segment (or middle tibia alone) clothed with conspicuous rows of long hairs. Hind coxa longer than wide. Winged forms unknown.

The following two genera belong to this tribe:

Asclepios Distant, *Halobates* Eschscholtz.

(*b*) METROCORINI Matsuda, new tribe

Fresh water habitat. Body surface smooth. Clypeus with basal margin lost. Middle tibia and first tarsal segment without conspicuous mass of hairs. Hind coxa wider than long. Winged forms occur.

The following genera belong to this tribe:

Metrocoris Mayr, *Eurymetra* Esaki, *Eurymetropsis* Poisson, *Eurymetropsiella* Poisson, *Eurymetropsielloides* Poisson, *Ventidius* Distant including two subgenera (*Ventidius* Distant *s. str.* and *Ventidioides* Hungerford and Matsuda), *Esakia* Lundblad.

SUBFAMILY RHAGADOTARSINAE LUNDBLAD

Forewing with R + M + Cu simply branched into two apical veins beyond middle of wing, always with pale line of weakness horizontally at middle of wing. Definitive intersegmental suture represented by posterior margin of mesothoracic postnotum and metacetabular suture. Lateral suture separating mesonotum from mesopleuron always present. Genae well developed (lobate). Omphalium absent. First abdominal segment ventrally well retained. Ovipositor well formed.

The following genera belong to this subfamily:

Rhagadotarsus Breddin including two subgenera (*Rhagadotarsus* Breddin *s. str.*, *Caprivia* China), *Rheumatobates* Bergroth including two subgenera (*Rheumatobates* Bergroth *s. str.*, *Hynesia* China).

SUBFAMILY TREPOBATINAE MATSUDA, *new subfamily*

Forewing with R + M + Cu simply branched into two apical veins, always with horizontal line of weakness at middle of wing. Definitive intersegmental suture dorsally represented by posterior margin of mesothoracic postnotum and laterally by metacetabular suture. Lateral longitudinal suture separating mesonotum from mesopleuron absent. Genae not lobately developed. Omphalium absent in most species. First abdominal segment ventrally absent. Ovipositor not formed.

The following genera belong to this subfamily:

Trepobates Uhler, *Stenobates* Esaki, *Rheumatometroides* Hungerford and Matsuda, *Cryptobates* Esaki, *Telmatometra* Bergroth, *Trepobatoides* Hungerford and Matsuda, *Ovatametra* Kenaga, *Halobatopsis* Bianchi, *Rheumatometra* Kirkaldy, *Hynesionella* Poisson, *Metrobatopsis* Esaki, *Naboandelus* Distant, *Metrobates* Uhler.

In the above new classification *Amemboa, Platygerris, Charmatometra,* and *Brachymetra* have been transferred from the Halobatinae to the Gerrinae. *Amemboa* and *Platygerris*, in spite of their relatively short size and round inner margin of the eye, are nothing but highly specialized genera of Eotrechini and Cylindrostethini respectively. They are closer to *Onychotrechus* and *Potamobates* of the Gerrinae respectively than to any genera of Halobatinae. *Charmatometra* and *Brachymetra* are also structurally much closer to Gerrinae than to any genus of Halobatinae. They are, therefore, transferred to the Gerrinae in spite of relatively short body size and round eyes, and a new tribe Charmatometrini is erected to receive these two genera and *Eobates*. Halobatinae, after removal of the above genera, is further divided into two subfamilies, *i. e.*, Halobatinae and Trepobatinae. The subfamilies are quite distinct in some fundamental characters as noted from the foregoing diagnoses. The two subfamilies are, in fact, not closely related. The Hermatobatinae is excluded from the Gerridae in this new classification, since this group is obviously very different from the rest in the basic structural plan, as will be discussed more fully elsewhere. No further taxonomic treatment of this group other than the exclusion from the Gerridae is attempted here.

Relationships of subfamilies

Since the known fossils of the Gerridae are members of modern genera (*Metrobates*, *Gerris*) they do not contribute information to phylogeny or relationships of groups of Gerridae. The understanding of relationships of subfamilies thus can be made only on the basis of the information presented in the section of the structural evolution in this work.

The subfamilies of the Gerridae are well defined and the family Gerridae appears to be considerably heterogeneous. No one subfamily is a direct ancestor nor do they seem to be derivatives one from another. In spite of this heterogeneity there appears to be definitely two main groups in the Gerridae, *i. e.*, the group including the Rhagadotarsinae and Trepobatinae on one hand and another group including the three other subfamilies on the other. The Rhagadotarsinae and Trepobatinae share two very fundamental characters in common, *i. e.*, the definitive intersegmental suture between the mesonotum and metanotum of the same morphological nature, and the occurrence of a line of weakness on the hemelytra. The sharp increase of growth ratios for the antennal and leg segments, which were found in a representative species of each subfamily, also indicates their close relationship. In spite of these similarities the two subfamilies are well differentiated from each other by certain characters, such as the retention of the first abdominal segment ventrally, formation of the well-developed ovipositor in Rhagadotarsinae. The other group comprising three subfamilies is more heterogeneous than the first group. The Gerrinae and Ptilomerinae are apparently closer to each other than they are to the Halobatinae. The primary intersegmental suture between the mesonotum and metanotum is retained in all species of Ptilomerinae, while it has been lost laterally in varying degrees in various tribes in the Gerrinae. The forewing venation is also definitely more primitive than in the Gerrinae. In spite of retention of these two highly primitive characters, the Ptilomerinae has evolved to become a distinct subfamily by acquiring some peculiar characters in the legs and antennae, obviously in adaptation to the peculiar habitat (swift and turbulent currents). Due probably to a strong predilection for this peculiar habitat, wider distribution of this subfamily must have been prevented. It occurs only in the tropical oriental region and Madagascar. The Halobatinae, though closer to the Gerrinae than to the others, is still remotely related. Important characters such as the different morphological origin of the intersegmental suture between the mesonotum and metanotum distinguish it from any other subfamily of the Gerridae; its extremely reduced metasternum cannot directly be derivable from any form of the Gerrinae known, but the proportional lengths of leg segments as well as the growth pattern for the antennal and leg segments (especially the fact that the growth ratios for the segments rather abruptly decrease at the

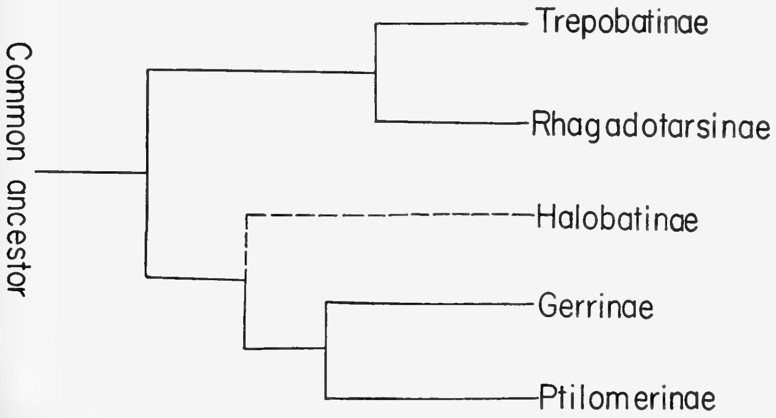

DIAGRAM 1.—Diagram showing the relationships of subfamilies of the Gerridae.

final stage of development in *Metrocoris histrio*), the fact that the metacetabular suture is not well developed dorsally, etc., lead one to suppose that this subfamily is at least closer to the Gerrinae than either to the Rhagadotarsinae or to the Trepobatinae.

The above discussion on the relationships of subfamilies of the Gerridae can be summarized in diagram 1.

SUBFAMILY GERRINAE AMYOT AND SERVILLE

Gerrinae Bianchi, Ann. Mus. St. Petersbourg for 1896, p. 69 (1896)
Gerrinae Lundblad, Arch. Hydrobiol. Suppl. 12:374(1933)
Gerrinae Drake and Harris, Ann. Carnegie Mus., 23:181(1942)
Gerrinae Kuitert, Univ. Kansas Sci. Bull., 28(7):116(1942)
Gerritae Kirkaldy, Ann. Soc. Ent. Belg., 43:509(1899)
Gerrinaria Distant, Faun. Brit. Ind., Rhynch., 2:176(1903)
Gerrini Torre-Bueno, Trans. Amer. Ent. Soc., 37:244(1911)

Structures in wingless forms: Body large and elongate. Head with clypeal region always produced, basal margin of clypeus distinct or lost. Eye indented, not covering anterolateral angle of pronotum in most genera. Antenniferous tubercle well developed in most genera; antennal cavity open anterior to eyes. Antenna slender in most genera; first segment longest in most genera; second segment about as long as or longer than third except for Charmatometrini in which third always longer than second; third segment always with small but distinct accessory segment (basal peduncle); fourth segment simple and long, or short and curved (Cylindrostethini). Mandibular and maxillary plates more or less distinct from each other in most genera. Rostrum either extending or not extending beyond prosternum.

Pronotum prolonged or not prolonged. Intersegmental suture between mesonotum and metanotum dorsally represented by true posterior margin of mesonotum, laterally absent or continuous with conspicuous metathoracic spiracle, which is nearly cephalocaudally placed. Longitudinal mesopleural suture separating mesonotum from mesopleuron completely absent in most genera. Mesosternum with paired longitudinal sutures separating mesosternum from mesopleuron present in some species of some genera. Metanotum with median longitudinal sulcus present in most genera. Metacetabular suture connected with intersegmental suture between mesonotum and metanotum dorsally in Cylindrostethini or not much extending dorsally in other tribes. Metasternum at least longer than first definitive abdominal ventrite (second abdominal ventrite). Omphalium present in all genera; omphalial groove leading onto metacetabulum present in some genera. Front leg with femur simple in most genera, always a little longer than tibia; tibia with or without conspicuous process at inner apical angle; tarsus with first segment greatly reduced only in Cylindrostethini; claws arising preapically in most genera. Middle leg longer than hind leg in great majority of species; femur longer than tibia in most genera; first tarsal segment longer than second except in *Onychotrechus.* Hind leg with femur longer than tibia in great majority of species; first tarsal segment longer than second in great majority of species.

Abdomen elongate. First tergite with anterior margin either straight or flattened W-shaped; first ventrite absent. Connexivum nearly horizontal or reflexed, with or without connexival spine, ventral margin of connexivum distinct in many genera. Definitive first connexival segment is the fused first and second connexival segments.

Male: Seventh segment longer than sixth segment in many species, variously modified in some species. Eighth segment often greatly prolonged. Ninth segment with suranal plate simple on lateral margin in most species; pygophore with apical margin simply rounded in majority of species; parameres simple and well developed or greatly reduced. Endosoma variable in various groups.

Female: Seventh segment longer than sixth in most species, ventral apical margin greatly modified in some genera. First valvula split into two lobes. Second valvulae convergent apically; intervalvular membrane with apical margin strongly sclerotized in Cylindrostethini.

Winged forms: Hemelytra with Sc connected with R + M by oblique vein Sc_2 at the point of separation into R and M, or connected with R + M; Vein A connected with posterior margin of hemelytra by a short, obscure cross vein. Line of weakness absent.

Distribution: World-wide.

Relationships of tribes.

The Cylindrostethini shares 15 characters * in common with the Gerrini, more characters than with any other tribe, indicating a closer relationship. Primitive genera of both tribes have highly elongate bodies. The Cylindrostethini, as will be noted from the table, has the smallest number of primitive characters although this tribe retains such obviously primitive features as the omphalial

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* (±)^{x} sign is here regarded as (+), since (—) alternatives are shared only by some specialized forms of each tribe.

TABLE 6.—Table of significant tribal characters in Gerrinae.

	Gerrini	Cylindrostethini	Eotrechini	Charmatometrini		Gerrini	Cylindrostethini	Eotrechini	Charmatometrini
10	(+)	(—)	(+)	(+)	62A	(±)$^{\times}$	(±)$^{\times}$	(+)	(+)
23	(+)	(—)	(+)	(+)	63B	(±)$^{\times}$	(±)$^{\times}$	(+)	(+)
24	(±)$^{\times}$	(—)	(—)	(+)	68A	(±)$^{\times}$	(—)	(±)$^{\times}$	(+)
29	(+)	(±)$^{\times}$	(+)	(+)	69A,B	(—)	(—)	(±)$^{\times}$	(+)
33	(±)$^{\times}$	(+)	(+)	(±)$^{\times}$	72A	(+)	(±)$^{\times}$	(+)	(+)
34A	(+)	(—)	(+)	(+)	74	(+)	(+)	(±)$^{\times}$	(+)
35	(—)	(—)	(—)	(+)	76	(—)	(—)	(±)$^{\times}$	(—)
42	(±)$^{\times}$	(±)$^{\times}$	(—)	(+)	102	(+)	(+)	(+)	(—)
48	(—)	(—)	(—)	(+)	112	(+)	(+)	(±)$^{\times}$	(+)
59	(±)$^{\times}$	(±)$^{\times}$	(—)	(—)	Total. .	(+) 8 (±) 8 (—) 4	(+) 4 (±) 7 (—) 9	(+)10 (±) 5 (—) 5	(+)16 (±) 1 (—) 3
61A	(±)$^{\times}$	(±)$^{\times}$	(+)	(+)					

For explanations of symbols see introduction and table 5.

groove in many species. Many more specialized characters peculiar to this tribe, such as the curved fourth antennal segment, the greatly reduced first tarsal segment of the front leg, the peculiar way of connection of the clypeus with the labrum, and the well developed metacetabular suture which is dorsally connected with the primary intersegmental suture between the mesonotum and metanotum make this tribe quite distinct from the others.

The Gerrini also shares 15 characters with the Charmatometrini and with the Eotrechini. The tribe thus shares the highest total number of characters with the other tribes (45), suggesting that it is probably the closest to the ancestral gerrine.

The Charmatometrini has the largest number of primitive characters (16), but this is due partly to the fact that this tribe has never diversified as much as in the other tribes, thus remaining relatively primitive as a whole. In fact the number of primitive characters in *Charmatometra,* the most primitive genus in this tribe, is about the same as in the primitive genera of the other tribes, such as *Eotrechus* and *Gigantometra*. The tribe Charmatometrini shares 14 characters with the Eotrechini, 10 with the Cylindrostethini, and 15 with the Gerrini. This indicates that this tribe, while it has evolved from near the base of gerrine phylogeny, is related to the Eotrechini. Both tribes are relatively small in body size and the spine of the seventh connexival segment has not arisen in either.

Based on the above discussion the relationships of the tribes are indicated in diagram 2.

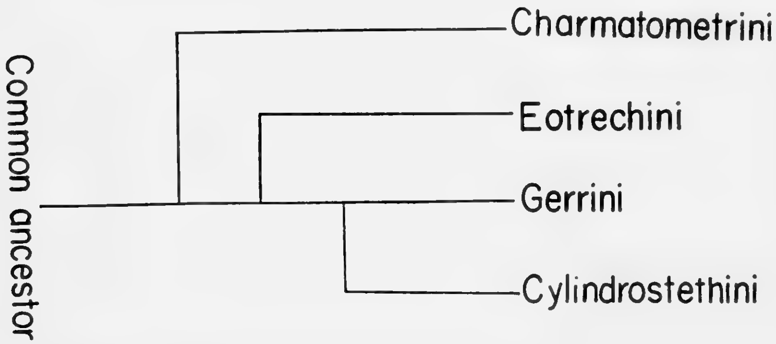

DIAGRAM 2.—Diagram showing the relationships of tribes of the Gerrinae.

Tribe GERRINI Amyot and Serville

Color pattern: Pronotum with either yellow or black median longitudinal and marginal stripes. Mesonotal and metanotal regions normally with silvery areas.

Structures in wingless forms: Head between eyes widened posteriorly. Clypeal region well produced anteriorly, basal margin of clypeus either distinct or indistinct, apical margin directly connected with base of labrum. Antennae shorter than body; first segment longest in most genera; third segment a little longer than second in most genera and with a small but distinct basal peduncle; fourth segment longer than third. Antenniferous tubercles well developed and somewhat divergent apically. Eye exserted, globular, inner margin more or less emarginated. Mandibular and maxillary plates usually distinct from each other. Rostrum extending beyond base of prosternum, third segment over two and a half times as long as fourth segment.

Pronotum prolonged in most genera. Mesosternum with median longitudinal sulcus distinct anteriorly; paired longitudinal sutures present in some species of some genera. Intersegmental suture between mesonotum and metanotum laterally retained, or directly continuous to conspicuous metathoracic spiracle, or obliterated. Metanotum with distinct medial longitudinal sulcus in most species; lateral longitudinal elevation well developed, reaching anteriorly nearly to mesonotum; metacetabular suture well impressed behind spiracle and dorsally meeting lateral longitudinal elevation. Metasternum with omphalium distinct; omphalial groove lost except in *Gigantometra* and *Gerriselloides.* Front leg with femur simple, a little longer than tibia; tibia simple, without conspicuous inner apical process; tarsus with first segment not strongly reduced in most species; claws arising preapically. Middle leg longer than hind leg except in *Gigantometra;* tibia 0.7 to 1.08 times as long as femur; tarsus with first segment 2.2 to 9.5 times as long as second segment. Hind leg with tibia 0.23 to 1.6 times as long as femur; first tarsal segment 1.1 to 3.25 times as long as second.

Abdomen elongate. First tergite with anterior margin flattened W-shaped; anterior limit of connexivum extending beyond anterior margin of first tergite; ventral margin of connexivum recognizable either as broken longitudinal suture or as depressions on each segment.

Male: Seventh segment with ventral apical margin either simply concave or with a small median emargination, or with a median process; ventral surface longitudinally elevated medially in some species. Eighth segment prolonged and modified on ventral surface in some species. Ninth segment with suranal plate simple in great majority of species; pygophore not rotated, simply rounded on apical margin; parameres greatly reduced. Endosoma strongly sclerotized and produced apically in some genera; definitive dorsal plate bent along apical margin of endosoma; ventral plate more or less membranous, bilobed or not bilobed.

Female: Seventh segment with ventral apical margin simply concave or produced medially, or more or less greatly produced and modified. First valvula rather thinly sclerotized, apex membranous and rounded, inner lobe well differentiated from outer lobe in most species. Second valvulae membranous apically and convergent (in *Tachygerris* both valvulae are greatly reduced); intervalvular membrane with apical margin not heavily sclerotized. Vulva membranous, simply rounded or with median apical projection.

Winged forms: Vein Sc_2 connected with R + M at point of separation into R and M, or joining R + M basal to that point. Vein A connected by a short cross vein with posterior margin of hemelytron.

Distribution: World wide.

TABLE 7.—Table of significant generic characters in Gerrini.

	Gigantometra	Aquarius	Gerris *s. str.*	Limnoporus	Gerrisella	Gerriselloides	Eurygerris	Limnogonus *s. str.*	Limnogonellus	Tachygerris	Limnometra	Tenagogonus	Tenagogerris	Tenagometra	Tenagometrella
9	(—)	(—)	(—)	(+)	(+)	(+)	(—)	(—)	(—)	(—)	(±)	(±)	(—)	(—)	(+)
11	(+)	(+)	(+)	(+)	(+)	(+)	(±)	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(+)
17	(+)	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
20	?	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(+)	(+)	(—)	(—)	(+)	(+)	(—)
24	(+)	(+)	(+)	(+)	(—)	(+)	(±)×	(+)	(±)×	(+)	(+)	(±)×	(+)	(—)	(+)
27	(+)	(±)×	(±)×	(±)×	(—)	(+)	(±)×	(±)×	(—)	(—)	(±)×	(—)	(+)	(—)	(—)
33	(±)	(±)	(±)	(±)	(—)	(±)	(+)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
42	(+)	(—)	(—)	(—)	(—)	(±)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
59	(+)	(+)	(±)×	(+)	(—)	(—)	(—)	(±)×	(—)	(±)×	(+)	(±)×	(—)	(—)	(+)
61B, C	(+)	(±)×	(±)×	(±)×	(+)	(+)	(—)	(+)	(+)	(+)	(±)	(±)	(+)	(+)	(+)
62A	(+)	(+)	(+)	(+)	(+)	(+)	(±)	(±)	(±)	(—)	(+)	(±)	(+)	(+)	(±)

TABLE 7.—Table of significant generic characters in Gerrini.—*continued.*

	Gigantometra	Aquarius	Gerris *s. str.*	Limnoporus	Gerrisella	Gerriselloides	Eurygerris	Limnogonus *s. str.*	Limnogonellus	Tachygerris	Limnometra	Tenagogonus	Tenagogerris	Tenagometra	Tenagometrella
63A, B........	(+)	(±)$^{\times}$	(±)$^{\times}$	(±)$^{\times}$	(—)	(+)	(—)	(±)$^{\times}$	(+)	(+)	(±)$^{\times}$	(±)$^{\times}$	(+)	(+)	(+)
68A...........	(+)	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(±)	(+)	(+)	(±)	(+)	(+)	(+)
73............	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(±)$^{\times}$	(+)	(±)$^{\times}$	(+)	(+)	(+)
86............	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(+)	(+)
92............	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(+)	(+)	(—)	(+)	(+)	(+)	(?)	(+)
97............	(+)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
101...........	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(+)	(+)	(±)$^{\times}$	(+)	(+)	(+)	(—)	(+)
117...........	O	O	O	O	O	O	O	O	O	×	×	×	×	×	O
120...........	O	O	O	O	×	×	O	O	O	O	O	O	O	O	O
121...........	×	×	×	×	O	×	O	O	O	O	O	O	O	O	O
124...........	2:1	2.3–2.9 :1	2.1–2.9 :1	2.1–2.5 :1	4:1	2:1	2–3.5 :1	2.8–4.4 :1	3.7–4.8 :1	3.5–4.1 :1	3.0–3.9 :1	3.1–5.7 :1	4(+):1	?	3.5:1

TABLE 7.—Table of significant generic characters in Gerrini.—*concluded.*

	Gigantometra	Aquarius	Gerris *s. str.*	Limnoporus	Gerisella	Gerriselloides	Eurygerris	Limnogonus *s. str.*	Limnogonellus	Tachygerris	Limnometra	Tenagogonus	Tenagogerris	Tenagometra	Tenagometrella
125	1.2:1	0.67–1.26 :1	0.5–1.0 :1	0.7–1 :1	0.25–0.35 :1	0.67:1	0.8–1 :1	0.5–1.0 :1	0.33–0.6 :1	0.83–1 :1	0.84–1.9 :1	0.6–0.9 :1	0.5:1	0.75:1	1:1
126	0.9:1	0.80–0.98 :1	0.76–0.92 :1	0.76–0.86 :1	0.93:1	0.70:1	0.78–0.97 :1	0.82–0.96 :1	0.88–0.97 :1	0.70–0.78 :1	0.78–1.08 :1	0.71–0.89 :1	0.94:1	0.93:1	0.99:1
127	9.5:1	2.9–8:1	1.7–3.3 :1	4.0–4.8 :1	3.1–3.3 :1	2.2:1	4.6–6 :1	3.3–5.4 :1	3–4.3 :1	5.3–6:1	3.9–7:1	3.5–4.7 :1	4.2:1	5.37:1	4.0–4.37 :1
128	1.54:1	0.57–0.87 :1	0.45–0.65 :1	0.42–0.62 :1	0.23–0.27 :1	0.55:1	0.44–0.61 :1	* 0.42–0.77 :1	0.40–0.55 :1	0.35–0.48 :1	0.58–1.0 :1	0.43–0.60 :1	0.55:1	0.54:1	0.43–0.55 :1
129	3.75:1	1.7–2.8 :1	1.6–2.0 :1	1.9–2.6 :1	1.1:1	2.0:1	1.7–2.3 :1	1.3–2.4 :1	1.6–2.2 :1	1.6–2.5 :1	1.8–3.3	1.1–1.8 :1	2.0:1	1.6:1	2.1:1
Total	(+) 15 (±) 1 (—) 1 (?) 1 (O) 2 (X) 1	(+) 10 (±) 4 (—) 4 (O) 2 (X) 1	(+) 10 (±) 5 (—) 3 (O) 2 (X) 1	(+) 12 (±) 4 (—) 2 (O) 2 (X) 1	(+) 9 (±) 0 (—) 9 (O) 2 (X) 1	(+) 14 (±) 2 (—) 2 (O) 1 (X) 2	(+) 6 (±) 4 (—) 8 (O) 3	(+) 10 (±) 4 (—) 4 (O) 3	(+) 9 (±) 3 (—) 6 (O) 3	(+) 7 (±) 3 (—) 8 (O) 2 (X) 1	(+) 10 (±) 4 (—) 4 (O) 2 (X) 1	(+) 5 (±) 8 (—) 5 (O) 2 (X) 1	(+) 13 (—) 5 (O) 2 (X) 1	(+) 8 (—) 9 (?) 1 (O) 2 (X) 1	(+) 12 (±) 1 (—) 5 (O) 3

* *Limnogonus intermedius* Poisson, a deviated species.

For explanations of symbols see introduction and table 5.

Relationships of Genera

On the basis of the difference in location of the metathoracic spiracle, the tribe can be divided into two major groups, one with the spiracle anteriorly approximated to the pronotum (*Gigantometra, Aquarius, Gerris s. str., Limnoporus* and *Gerriselloides*); the other with the metathoracic spiracle located at some distance from the pronotum (other genera). In the first group, *Gigantometra* retains the largest number of primitive characters, such as the omphalial groove, enormously large body size, etc., and this genus is probably closest to the ancestor of the first group of the Gerrini. *Aquarius* and *Gerris s. str.* are closely related to *Gigantometra,* although they are structurally more specialized and the growth patterns for the antennal and leg segments are probably considerably different from those in *Gigantometra. Gerriselloides,* though related to *Gerris s. str.,* is an aberrant and more primitive group represented by a single species. It retains the omphalial groove which is laterally obliterated on the metacetabula, has a short pronotum and the relatively long metasternum. *Limnoporus* is closely related to *Aquarius* but distinct from it by a few minor structural differences and apparently different growth patterns for many leg and antennal segments.

Among the genera of the second group, Australian *Tenagogerris* shares the largest number of characters with other genera. This genus is structually relatively primitive and similar to the *Limnometra-Tenagogonus* complex in color pattern, but similar also to *Gerris* in certain features, such as the short rostrum, similar proportional lengths of the first three antennal segments. This genus may possibly be the closest to the ancestral group of the Gerrini. *Tenagogonus* is nothing but a specialized group of *Limnometra. Tenagometra* has apparently become distinct from *Tenagogonus* with reduction of the pronotum in the wingless forms, etc., *Tenagometrella* is related to *Limnometra. Gerrisella* appears to be related to *Gerris s. str.,* but the difference in location of the metathoracic spiracle, the relatively short middle and hind tibiae, etc., which must have resulted from a considerably different growth pattern, the completely reduced pronotum in wingless forms, etc., make this genus quite peculiar and distinct. As will be noted from table 7, *Gerrisella* does not share large enough number of characters with any other genera to suggest any close relationship. *Limnometra s. str.* is similar to *Gerris* in color pattern, but is different in the location of the metathoracic spiracle, etc. *Limnogonellus,* though closely related to *Limnogonus s. str.,* has apparently become distinct from it by minor alteration in the growth patterns for the antennal segments and by a different process of evolution of the male eighth abdominal segment, etc.

The last two genera occurring in the Western Hemisphere, *Eurygerris* and *Tachygerris*, are divergent in many respects. *Eurygerris*, though formerly included in *Gerris*, is quite distinct by the different location of the metathoracic spiracle, retention of the primary intersegmental suture between the mesonotum and metanotum laterally, the different lengths of the antennal and leg segments in relation to the body size, a strong tendency towards reduction of the pronotum, etc. As will be noted from table 7, *Eurygerris* does not have a large enough number of characters in common with any group to show any close phylogenetic relationship, and the total number of characters it shares with other genera is one of the smallest. *Tachygerris*, although unique in the modification of the female seventh abdominal segment and in the female and male genitalia, etc., is more closely related to the *Limnometra-Tenagogonus* complex than to the other genera.

The relationships of genera in the Gerrini discussed above can be summarized in the following diagram 3.

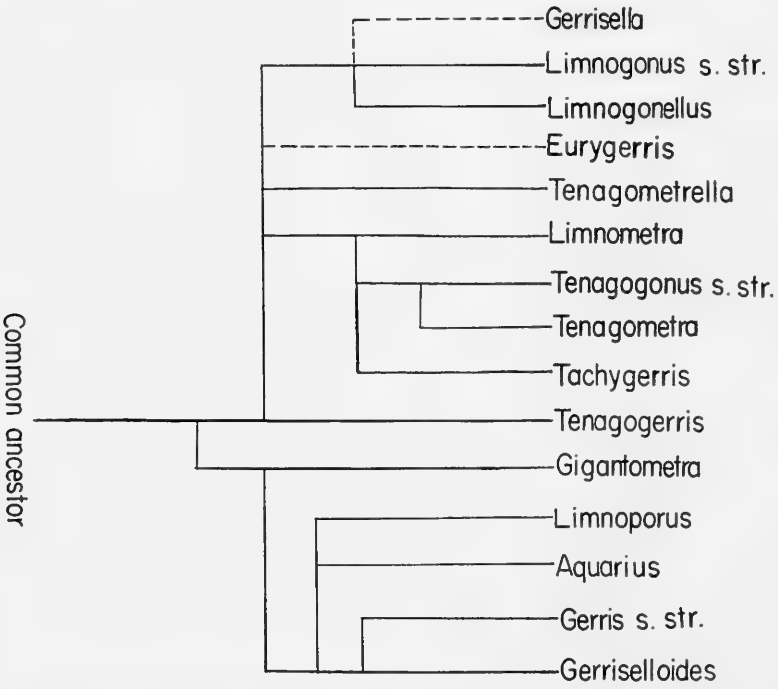

DIAGRAM 3.—Diagram showing the relationships of genera of the Gerrini.

The evolutionary tendencies and characters more or less peculiar to the Gerrini

(1) The pronotum is always prolonged in primitive wingless forms, but it has become reduced in the more specialized genera.

(2) The venter of the mesothorax has the paired longitudinal sutures separating the mesosternum from the mesopleural regions retained in the more primitive species of more primitive genera; they have become lost in more specialized forms.

(3) The primary intersegmental suture between the mesonotum and metanotum is laterally retained only in *Eurygerris, Onychotrechus,* and *Chimarrhometra.* In other genera it is laterally either occupied by the metathoracic spiracle which is anteriorly approximated to the pronotum, or has become lost.

(4) The omphalial groove and its lateral opening on the metacetabula are retained in *Gigantometra;* the groove is retained but its lateral openings are lost in *Gerriselloides;* both the groove and the lateral opening are completely lost in the other genera.

(5) The connexival spine is retained in the more primitive genera or more primitive species of some genera. It has become highly reduced or lost in the more specialized forms.

(6) The second to seventh abdominal spiracles are located closer to the anterior margin than to the posterior margin of each segment in the more primitive species of the more primitive genera. They have become placed at the middle between the anterior and posterior margins of each segment in the more specialized forms.

(7) The vein Sc has become connected with R + M basal to the point of separation into R and M in more specialized forms.

(8) In the middle leg, there is evidence that the allometric growth slope for the tibia is about as steep as or gentler than that for the femur, and this growth pattern appears to have persisted in phylogeny of at least a great majority of genera.

(9) In the hind leg, the tibia has become shorter in relation to the femur in more specialized forms.

Genus *Gigantometra* Hungerford and Matsuda

(Figs. 3, 171-178)

Gigantometra Hungerford and Matsuda, Jour. Kans. Ent. Soc., 31(2):115-117 (1958).
Limnometra China, Bull. Brooklyn Ent. Soc., 20(5):218-220(1925) (in part).
Limnometra Hoffmann, Lingnan, Sci. Jour., 15(3):489-492(1936) (in part).

Type species: *Limnometra gigas* China, by original designation.
Species examined: *Gigantometra gigas* (China).

Color pattern: Predominantly black. Head with pale, crescent shaped mark at base, a pair of lateral and median black stripes confluent anteriorly. Pronotum with median pale longitudinal stripe extending onto posterior lobe, lateral margin with pale stripe. Mesopleural region with longitudinal stripe of silvery pubescence.

Structures in wingless forms: Largest gerrid known. Head including eyes wider than long. Eye exserted, strongly indented, rather small and globular. Antenna slender, considerably shorter than length of body; first segment much shorter than second and third segments together; second segment short, third segment longer than second and than fourth; fourth segment about half as long as first. Antenniferous tubercles subparallel, about as long as eye. Clypeus with basal margin indistinct. Mandibular and maxillary plates distinct from each other. Rostrum extending beyond prosternum; first segment about one third as long as head, third segment over four times as long as fourth segment.

Pronotum fully prolonged, apical margin rounded. Mesothorax strongly widened posteriorly. Intersegmental suture between mesonotum and metanotum laterally continuous to conspicuous metathoracic spiracle. Mesosternum a little less than twice as long as metasternum; median longitudinal sulcus distinct in anterior third; paired longitudinal sutures distinct in anterior two thirds of mesosternum. Metathoracic spiracle very conspicuous, obliquely placed. Metanotum with lateral longitudinal elevation distinct, median longitudinal sulcus shallowly impressed. Metasternum with distinct omphalium located at apical one sixth of metasternum, omphalial groove leading onto metacetabula well impressed, lateral opening clothed with tuft of straight hairs. Front leg with femur slender, subequal in breadth throughout, a little longer than tibia; tibia slender, a little thickened apically, with a slight constriction near apex, and with obscure, bare and shallow depression on inner surface near apex. Middle leg a little less than three times as long as body, femur only slightly longer than tibia; tibia a little less than four and a half times as long as first tarsal segment; first tarsal segment almost ten times as long as second. Hind leg much longer than middle leg; femur about as long as middle femur; tibia over one and a half times as long as femur, over twenty-five times as long as first tarsal segment; first tarsal segment a little less than four times as long as second.

Abdomen long. First abdominal tergite with flattened W-shaped anterior margin; second to seventh tergites subequal in length, each a little longer than wide; first to sixth ventrites subequal in length; seventh segment with connexival spines conspicuous in both sexes. Abdominal spiracles placed much closer to anterior margin than to posterior margin of each segment. Ventral longitudinal margin of connexivum distinct, broken at anterior one third and not reaching posterior margin of each segment. Ventral median longitudinal impression distinct throughout.

Male: Seventh segment with ventral apical margin simply concave. Eighth segment slightly exposed ventrally, simple on ventral surface. Ninth segment with suranal plate simply narrowed near apex, with a fine foot-shaped process on basal region of each side; pygophore rather small, feebly notched at middle of apical margin; parameres robust and simple, relatively short. Endosoma with dorsal plate slender, forked basally (the part of basal plate); apical plate not fused with dorsal plate; ventral plate membranous; lateral plates slender.

Female: Not available for study.

Winged forms: Metathoracic spiracle approaching nearly to wing base. Pronotum elongate, humeri located behind middle of pronotum. Hemelytra with Sc connected with R + M at the point of separation into R and M.

(The description of the dorsal surface of the body is based on the illustration of the wingless form given by Hoffmann, 1936.)

Distribution: The oriental region (Hainan Island, Tonking).

This monotypic genus is more primitive than any other genera of the Gerrini in the following points:

(1) The omphalium and the omphalial groove are clearly retained.

(2) The mesosternum is only a little less than twice as long as the metasternum.

(3) The hind leg is longer than the middle leg.

(4) The parameres are better developed than in any other species of the tribe examined.

Besides the above mentioned characters peculiar to this genus, the extraordinarily long body and legs separate this genus readily from the other genera of the tribe.

Genus *Gerris* Fabricius

Gerris Fabricius, Ent. Syst., 4:187(1794)
Gerris Latreille, Consid. Génl., pp. 259, 434(1810)
Gerris Van Duzee, Cat. Hemip., 1:426(1917)
Gerris Drake and Harris, Ann. Carnegie Mus., 23:182-202(1934)
Gerris Kuitert, Univ. Kansas Sci. Bull., 28(1):117-125(1942)
Gerris Stichel, Illust. Best. Wanz., 4:109-123(1955)
Hydrometra Lamarck, Syst. Anim. s. Vert., p. 295(1801) (in part)
Ures Distant, Faun. Brit. Ind., Rhynch., 5:149-150(1910) (type species, *U. custos* Distant)

Type species: *Cimex lacustris* Linnaeus, by subsequent designation (Latreille 1810, in the above reference).

Color pattern: Head with a crescent shaped yellow marking at base. Pronotum with yellowish median longitudinal stripe either extending onto or not extending onto posterior lobe. Mesopleural and metapleural regions silvery pubescent.

Structures in wingless forms: Head including eyes wider than long. Vertical region strongly widened. Eye with inner margin strongly emarginated. Antenna slender, definitely shorter than length of body; first segment a little longer than or shorter than two following segments together; second segment as long as or longer than third; fourth segment always longer than third segment. Antenniferous tubercles either as long as or shorter than eye. Clypeus with basal margin indistinct. Mandibular and maxillary plates distinct from each other. Rostrum extends beyond prosternum; third segment over two and a half times to a little over four times as long as fourth segment.

Pronotum prolonged, lateral margin slightly concave at middle, posterior margin broadly rounded. Intersegmental suture between mesonotum and metanotum laterally occupied by metathoracic spiracle which reaches anterodorsally nearly to pronotum. Mesosternum twice to three times as long as metasternum, with a distinct median longitudinal sulcus anteriorly; paired longitudinal sutures distinct anteriorly in some species. Metanotum with lateral longitudinal elevation distinct, median longitudinal sulcus distinct. Metasternum with omphalium reduced but distinct; lateral omphalial groove absent. Front leg with femur simple, a little longer than tibia; tibia with inner apical process inconspicuous; tarsus with first segment one and one fourth to one half as long as second segment; second segment with claws arising preapically. Middle leg with femur about as long as to one and one fourth times as long as tibia; tibia over four times to a little over one and a half times as long as first tarsal segment; first tarsal segment a little less than twice to almost eight times as long as second tarsal segment. Hind leg shorter than middle leg, femur over twice to a little longer than tibia; tibia a little less than three times to about five times as long as first tarsal segment in most species. (In *ventralis* seven times as long as first tarsal); first tarsal segment a little over one and one half to almost three times as long as second tarsal segment.

Abdomen elongate. First tergite with anterior margin W-shaped (or bisinuate); second to seventh tergites nearly equal in length in most species; first to sixth ventrites subequal in lengths in most species. Seventh segment with connexival spine present in both sexes of many species. Abdominal spiracle placed either closer to anterior margin than to posterior margin, or at middle of each segment; ventral connexival suture present; ventral median longitudinal impression distinct throughout.

Male: Seventh segment with ventral apical margin simply concave or with a median small emargination on concave ventral apical margin. Eighth segment with more or less conspicuous median longitudinal elevation on ventral surface in most species. Ninth segment with suranal plate simple; pygophore well exposed, with simple apical margin; parameres highly reduced but recognizable. Endosoma more or less strongly sclerotized and produced apically in many species; definitive dorsal plate extends apically along apical margin of endosoma; ventral plate more or less membranous, bifurcate or not bifurcate apically.

Female: Seventh segment with ventral apical margin simply concave or feebly produced medially. Eighth segment ventrally always well exposed. First valvula with well differentiated inner lobe of varying lengths, apex of outer lobe either acute or rounded. Second valvulae lobate or simply narrowed apically, directed mesad beyond apical margin of intervalvular membrane.

Winged forms: Sc normally connected with R + M at the point of branching into R and M. Pronotum with humeri located behind middle.

Distribution: World-wide. The study of more material is necessary before clear distributional pattern for each subgenus can be obtained.

Subgenus *Aquarius* Schellenberg

(Figs. 15, 65-71, 74-75, 82-85, 88-89, 91-95, 98-101, 106, 109, 111, 129, 148, 165, 179-186, 193, 195, 196, 204, 206, 208, 211-220)

Aquarius Schellenberg, Gesc. Land u. Wass. Wanz., p. 25(1800).
Aquarius Kirkaldy, Trans. Amer. Ent. Soc., 32:155(1906).
Aquarius Bueno, Trans. Amer. Ent. Soc., 37:244(1911).
Aquarius Bergroth, Proc. U. S. Nat. Mus., 51:237(1916).
Aquarius Van Duzee, Cat. Het., 1:426-427(1917).
Aquarius Esaki, Entomologist, 59:273(1926) (as genus).
Aquarius Poisson, Bull. Soc. Sci. Bretagne, 17(3-4):9, 13(1940) (as genus).
Aquarius Hoffmann, Lingnan Sci. Jour., 20(1):23-25(1941) (as genus).
Aquarius Hoberlandt, Acta Ent. Mus. Nat. Pragae, 26(352):34(1948).
Aquarius Kiritschenko, Heteroptera of the European part of the Soviet Union (in Russian) (1951) (as genus).
Hygrotrechus Stål Öfv. Vet. Akad. Förh., 25:395(1868) (type species, *Cimex najas* (De Geer).

Type species: *Gerris paludum* Schellenberg 1800 nec Fabricius 1794 = *Cimex najas* De Geer, by subsequent designation (Kirkaldy 1906).

Species examined: G. (A.) *amplus* Drake and Harris, G. (A.) *antigone* Kirkaldy, G. (A.) *chilensis* (Berg), G. (A.) *conformis* (Uhler), G. (A.) *elongatus* (Uhler), G. (A.) *nebularis* Drake and Hottes, G. (A.) *nyctalis* Drake and Hottes, G. (A.) *najas* (De Geer), G. (A.) *remigator* (Horváth), G. (A.) *remigis* Say, G. (A.) *stappersi* (Poisson), G. (A.) *spinolae* Lethierry and Severin, G. (A.) *ventralis* (Fieber).

Color pattern: Pronotum with a median longitudinal stripe only in anterior half, with yellow lateral margin usually between humeri and anterior lobe (total posterior margin in *spinolae*) in winged forms. Thorax ventrally with adpressed silvery hairs.

Structures in wingless forms: Antenniferous tubercles subparallel, about as long as eyes. Antenna with first segment always longer than second and third segments together; second segment a little longer than or equal to third. Clypeus with basal margin more or less obliterated. Mandibular and maxillary plates distinct from each other although usually densely clothed with long hairs; the former overlaps basal upper part of the latter. Rostrum thick; third segment between three and four times as long as fourth segment. Ventral surface of head densely clothed with long silvery hairs.

Pronotum with anterior margin straightly elevated between eyes; anterior lobe distinct from posterior lobe by an obscure transverse depression; posterior lobe entirely covering mesonotum, broadly rounded on apical margin; lateral margin slightly sinuate; upper surface usually with a median longitudinal carina of the same color as ground color, or of darker color. Mesosternum about two and a half times as long as metasternum in most species, never more than three times as long as metasternum; median longitudinal sulcus distinct anteriorly; paired longitudinal sutures divergent posteriorly, more or less distinct in all species. Metanotum with median longitudinal sulcus distinct in most species; metacetabular suture meets dorsally with lateral longitudinal elevation. Metasternum with posterior margin concave; omphalium placed close to posterior margin of metasternum. Front leg with femur straight, occasionally dorsoventrally flattened in male (*e. g., chilensis*); tibia straight, slightly thickened apically, with a faint longitudinal depression on inner surface near apex; second tarsal segment not more than one and a half times as long as first segment. Middle leg with femur only slightly longer than tibia in most species; tibia about three and a half times as long as first tarsal segment in most species; first tarsal segment three to eight times as long as second segment. Hind leg with femur less than one and a half times as long as tibia in most species; tibia about five times as long as first tarsal segment in most species; first tarsal segment less than three times as long as second tarsal segment; second segment with distinct claws.

Abdomen narrow, with connexival spine conspicuous in most species, surpassing apical margin of eighth segment. First tergite shorter than second tergite, each abdominal tergite relatively long. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment; ventral longitudinal margin of connexivum distinct; ventral median longitudinal carina distinct at least in anterior segments in female.

Male: Seventh segment with ventral apical margin simply concave in some species, with an additional median emargination in many species; ventral surface simple. Eighth segment ventrally emarginated on apical margin in some species or produced medially in some species, with a conspicuous elevation of various shapes and degrees of development on ventral surface in most species; dorsal apical margin nearly straight or feebly concave. Ninth segment with suranal plate simple; pygophore rounded on apical margin; parameres reduced but distinctly recognizable. Endosoma with apical margin prolonged and more strongly sclerotized in many species; definitive dorsal plate curved ventrad along apical margin of endosoma, fused with robust bifurcate apical plate in many species; ventral plate membranous, bilobed in some species, the lobes fused together in some species. (Description of the genitalia is based on *najas, elongatus, cinereus, conformis, antigone, ventralis, amplus, nyctalis, remigis.*)

Female: Seventh segment ventrally broadly concave on apical margin in some species, slightly produced in some species. Eighth segment with valvifers together more or less produced at middle; surface smooth, or with oblique suture, or elevated along inner margin of each valvifer. First valvula with well differentiated inner lobe, apex of outer lobe rounded and membranous, with a spinous process in all species examined except for *chilensis.* Second valvula lobate apically, slightly extending beyond apical margin of intervalvular membrane, directed mesad and broadly rounded apically; intervalvular membrane with a pair of oblique sclerotized areas; ramus of second valvula fine. Vulva membranous and simply narrowed apically in most species. (Description of genitalia is based on *elongatus, cinereus, conformis, ventralis, remigis, amplus,* and *chilensis.*)

Modifications of the abdomen

The male seventh segment (figs. 193-196). In *elongatus, conformis, cinereus, chilensis, ventralis* the ventral apical margin is simply concave, and the segment is a little shorter than the sixth segment on the median longitudinal axis. The connexival spine is very conspicuous especially in the first two species. In *najas* and *antigone* the seventh segment is a little longer than the sixth ventrally and ventral apical margin is also concave; in *najas, remigator* and *uhleri* an incipient stage of modification of the segment is noted, *i. e.,* the ventral apical margin has become triangularly incised, and the seventh segment is distinctly longer than the sixth on the ventral longitudinal axis (7th:6th :: 10:9 in *remigator,* 12:10 in *najas*), or a little shorter than sixth (*uhleri,* 11:12). In *nyctalis, remigis, nebularis, amplus,* and *stappersi,* the ventral apical margin of the seventh segment has a median emargination, the seventh segment is definitely longer than the sixth ventrally, and the connexival spine is definitely less conspicuous than in other more primitive species. The relative lengths of the seventh and sixth segments range 13:12 in *nebularis* to 16:12 in *amplus* and 12:7 in *remigis* and *stappersi.*

The eighth abdominal segments (figs.193-196): The eighth segment is simple on the ventral surface in *elongatus, cinereus, conformis, ventralis,* etc., in which the seventh segment is also primitive; the eighth segment has a basal elevated area in *najas, remigator* and *uhleri;* in *nyctalis, remigis, amplus,* and *stappersi* the eighth segment is more or less greatly prolonged and the ventral surface is provided with a strong, longitudinal elevation throughout its entire length.

The ninth segment: The suranal plate as well as pygophore have remained relatively unmodified. The parameres are greatly reduced but distinctly recognizable in all species. The endosoma with its apical region is simple in the more primitive species like *elongatus* but the apical region has become greatly prolonged and more strongly sclerotized in more specialized species such as *remigis,* etc., as will be noted from the figures, 212-219.

The female seventh segment (figs. 204, 206, 208): In the female the degree of modification of the seventh segment is less than in the male. In *elongatus* the seventh ventrite is a little shorter than the sixth on the median longitudinal axis, the connexival spine surpasses the tip of the abdomen and the ventral apical margin is simply concave. This is the most primitive condition in this genus. In *uhleri, najas, cincereus,* etc., the segment is more or less similar to *elongatus.* In *remigis, amplus, nyctalis, conformis* the seventh ventrite is definitely longer than the sixth and the connexival spine has become considerably reduced.

The female eighth segment (figs. 204, 206, 208): In *elongatus* and a few other species (*nebularis, ventralis, najas*), in which the seventh segment is not much prolonged, the inner margin of each valvifer is elevated only apically. In *antigone, cinereus,* and *chilensis,* in which the seventh segment is equal to or only slightly longer than the sixth ventrite, the valvifer is not elevated along the inner margin and this condition appears to be the primitive one in this genus. In some other species such as *remigis, conformis, nyctalis* and *amplus,* in which the seventh segment is more or less greatly prolonged, the elevation is narrower than in *elongatus* but much more well marked, and this condition is the most specialized one in this genus.

Modification of the other structures

The antennae: The length of the second segment in relation to the third is greatest in the largest species, *elongatus,* and there is a striking tendency for the relative length of the second to the third to become smaller with reduction in the body size. The relative length of the second segment is smallest in the smallest species, *cinereus.* Slight deviation from the above tendency is, however, noted in three species, *remigis, amplus,* and *nyctalis,* all from the Western Hemisphere. In these species the relative length of the second segment is nearly the smallest in spite of the fact that they are relatively large sized species. The above noted tendency has apparently resulted, as we already observed, from a greater growth ratio for the second segment than for the third segment in this subgenus.

Deviations in some species

G. (A.) *remigis, amplus,* and *nyctalis,* all from the Western Hemisphere, are included in the subgenus *Aquarius* but they differ in certain structures from the rest of the species as follow:

(1) The lengths of middle and hind leg segments slightly deviate from the allomorphic slopes for these leg segments in this subgenus.

(2) In spite of the fact that they are relatively large in size, the male apical abdominal segments are highly specialized; among other species the abdomen is more primitive in the larger species and more specialized in the smaller species.

(3) The metasternum is relatively long, or relatively less reduced in comparison to other species although the abdomen is highly specialized.

(4) The first antennal segment is only slightly longer than the second and third segments together; while in all others the first segment is distinctly longer than the second and third segments together.

(5) The second and third segments are nearly equal in length; in other species the second segment is definitely longer than the third segment.

(6) The ventral side of the abdomen of the male is longitudinally impressed, instead of longitudinally carinated in the other species.

G. (A.) *stappersi* Poisson from Africa also has somewhat different lengths of antennal and leg segments and the more conspicuous connexival spine compared to the other species with equivalent body sizes.

Subgenus *Gerris* Fabricius *s. str.*

(Figs. 13, 111, 127, 129, 148, 165, 187-192, 194, 197-203, 205, 207, 209, 210, 221, 222)

Gerris Kirkaldy, Trans. Amer. Ent. Soc., 23:155(1906).
Gerris Kirkaldy and Torre-Bueno, Proc. Ent. Soc. Washington, 10:208(1908) (as genus).
Gerris Torre-Bueno, Trans. Amer. Ent. Soc., 37:244(1911).
Gerris Poisson,, Bull. Soc. Sci. Bretagne, 17(3-4):17(1940) (as genus).
Gerris Brown, Trans. Soc. Brit. Ent., 9(3):154(1948).
Gerris Hoberlandt, Acta Ent. Mus. Nat. Pragae, 26(352):33(1948).

Gerris Kiritschenko, Heteroptera of the European part of the Soviet Union (in Russian), pp. 100-101(1951) (as genus).
Limnotrechus Stål, Öfv. Vet. Akad. Förh., 27:395(1868) (as genus, type species, *Cimex lacustris* Linnaeus).
For other citations and type designation see generic bibliography.

Species examined: *G.* (*G.*) *alacris* Hussey, *G.* (*G.*) *argentatus* Schummel, *G.* (*G.*) *buenoi* Kirkaldy, *G.* (*G.*) *comatus* Drake and Hottes, *G.* (*G.*) *costae* (Herrich-Schaeffer), *G.* (*G.*) *firmus* Drake and Harris, *G.* (*G.*) *gibbifer* Schummel, *G.* (*G.*) *gillettei* Lethierry and Severin, *G.* (*G.*) *incognitus* Drake and Harris, *G.* (*G.*) *incurvatus* Drake and Hottes, *G.* (*G.*) *inseparatus* Drake and Hottes, *G.* (*G.*) *lacustris* (Linnaeus), *G.* (*G.*) *marginatus* Say, *G.* (*G.*) *odontogaster* (Zetterstedt), *G.* (*G.*) *pingreensis* Drake and Hottes, *G.* (*G.*) *thoracicus* Schummel.

Color pattern: Dark fuscous to black in ground color. Pronotum with a yellow median longitudinal stripe only on anterior lobe and often with yellow lateral margin. Front femur dark yellow, always with a black spot spreading usually almost entire length on outer surface. Connexivum always yellowish or red at least laterally.

Structures in wingless forms: Antenniferous tubercles as long as or a little shorter than length of eyes. Antenna relatively thick; first segment about as long as or a little shorter than second and third segments together; second and third subequal in length to each other. Basal margin of clypeus indistinct, widened apically. Mandibular and maxillary plates distinct from each other; the former apically covering upper basal region of the latter. Rostrum rather short; third segment always less than three times as long as last segment.

Pronotum with anterior margin broadly rounded, without conspicuous straight elevation as in *Aquarius;* anterior lobe distinct from posterior lobe by transverse obscure suture, lateral margin not or feebly sinuate behind anterior lobe, posterior lobe with broadly rounded apical margin; upper surface with narrow median longitudinal elevation. Mesosternum a little over twice to three times as long as metasternum, convex, median longitudinal sulcus distinct in anterior half; paired lateral sutures distinct in many species. Metanotum with median longitudinal sulcus distinct; lateral longitudinal elevation extend forward to meet metacetabular suture. Metasternum much longer than second ventrite. Omphalium highly reduced but distinct, located at about posterior one fifth of metasternum. Front leg with femur rather incrassate basally; tibia slightly thickened at apex, with shallow longitudinal depression on inner surface near apex. Second tarsal segment from one and a half to twice as long as first segment, claws arising from near apex. Middle leg with femur about one and two sevenths times as long as tibia except for *argentatus,* in which femur is just a little longer than tibia; tibia about twice as long as first tarsal segment in most species; first tarsal segment about three times as long as second tarsal segment in most species, less than twice as long as second segment in some species. Hind leg with femur about as long as or a little shorter than middle femur, usually about twice as long as tibia; tibia about three times as long as first tarsal segment in most species; first tarsal segment between one and a half to twice as long as second tarsal segment; apical claws recognizable as in middle leg.

Abdomen narrowed posteriorly. Connexivum with spine on seventh segment more or less greatly reduced, directed dorsad apically in some species. Abdominal spiracles placed closer to anterior than to posterior margin of each segment in most species, placed at middle between both margins in some species. Median ventral longitudinal carina distinct in most species; ventral longitudinal suture of connexivum interrupted at anterior third of each segment, the suture obscure and represented by shallow dot like depressions in some species.

Male: Seventh segment without connexival spine, ventral apical margin with double emargination in most species, with longitudinal depression on either side of median longitudinal axis in some species, with a pair of conspicuous tubercles near posterior margin at middle in *odontogaster.* Eighth segment with a conspicuous median longitudinal elevation on ventral surface in some species. Ninth segment with suranal plate simple; pygophore with apical margin simply rounded; parameres vestigial. Endosoma prolonged but not as much as in some species of *Aquarius* and not strongly sclerotized. Definitive dorsal and lateral plates as in *Aquarius;* ventral lobe long and slender, at least reaching apex of endosoma. (Description of the genitalia is based on *thoracicus, marginatus, firmus, odontogaster.*)

Female: Ventral apical margin of the seventh segment concave. Eighth segment with both valvifers together produced at middle in some species, upper surface with more or less distinct oblique sutures in some species. First valvula with well differentiated inner lobe of varying lengths in various species; apex of outer lobe simply narrowed apically, often acute at tip. Second valvula swollen and rounded at apex, slightly extending beyond apical margin of intervalvular membrane which is straight or straight with a small median notch. (Description of the female genitalia is based on *gillettei.*)

Modifications of the abdomen

(Figs. 197-203, 205, 207)

The process of modification of the abdomen can be traced, to a large extent, directly back to the abdomen of *Aquarius.*

The male seventh segment: In no species of *Gerris s. str.* is the seventh segment ventrally shorter than the sixth although this situation occurs in some species of *Aquarius.* In *thoracicus* (fig. 197) *costae, gibbifer* (fig. 194), *marginatus* and *lacustris* the seventh segment is as long as the sixth and this condition is the shortest or the least prolonged found in *Gerris s. str.* The ventral apical margin in these species is simply concave and without a distinct median notch, the connexival spine is clearly retained, and the ventral surface is unmodified. In *argentatus, buenoi,* and *inseparatus* the seventh segment is considerably longer than the sixth (6th:7th :: 8:9-10:13) but otherwise much as in the first group. In *argenticollis* (fig. 199), *incurvatus, comatus, incognitus,* and *alacris* the seventh segment is also considerably longer than the sixth, the ventral apical margin has a distinct median emargination and the connexival spine is more reduced, but the ventral surface is not conspicuously modified. In *gillettei* (fig. 201) and *pingreensis* (fig. 202) the seventh segment is also longer than the sixth segment, especially in *gillettei,* and the ventral surface is provided with well marked impressions along the median longitudinal elevation which extends the entire segment. In the last two species, *firmus* (fig. 200, 203) and *odontogaster* (fig. 198), the seventh segment is twice or almost twice as long as the sixth, and the ventral surface is greatly modified; the connexival spine in these species is absent.

The male eighth segment: In *thoracicus* (fig. 197), *marginatus, lacustris, gibbifer* (fig. 194), *costae,* and *inseparatus* the eighth segment has remained short and the ventral surface is relatively less modified. It has become more or less prolonged and with a more or less conspicuous longitudinal elevation in *gillettei* (fig. 201) and *pingreensis* (fig. 202). It is more strongly prolonged and the ventral surface is strongly longitudinally carinated and densely clothed with long adpressed hairs on either side of the median longitudinal elevation in *argenticollis* (fig. 199), *incurvatus, mar-*

ginatus, comatus, incognitus and *alacris.* The eighth segment is dorsally prolonged but ventrally relatively short and the ventral surface is not or only slightly modified in *firmus* (fig. 200) and *odontogaster* (fig. 198), although the seventh segment in these forms is highly modified. It should be noted that the trend in modification of the ventral surface of the eighth segment is similar to that of *Aquarius,* in which the median longitudinal elevation with adpressed long hairs on either side occur in somewhat divergent and specialized group including *G.* (*A.*) *remigis, G.* (*A.*) *amplus, G.* (*A.*) *nyctalis.* It is noted from the above description that the species with relatively long body are more primitive in the seventh and eighth abdominal segments than the species with shorter body.

The male ninth segment: As in *Aquarius* the ninth segment has remained simple. The apical segment of the endosoma has not become prolonged as in some species of *Aquarius.*

The female seventh and eighth segments: In all species examined the ventral apical margin of the seventh segment is more or less concave. The eighth segment, both valvifers together, more or less produced at the middle in *marginatus* (fig. 205), *incognitus, alacris, thoracicus, inseparatus, costae, gillettei, incurvatus, gibbifer* and *comatus.* In the last two species the surface of each valvifer has an oblique suture. It should be noticed that in all these species the sixth and seventh ventrites are more or less subequal in length. In all other species the posterior margin of each valvifer is emarginate laterally, and in some of these species the basal region of the valvifer is strongly depressed. In all these species the seventh ventrite is at least a little longer than the sixth; in *firma* it is much longer than the sixth.

The second to sixth ventrites: Compared with species of *Aquarius,* the abdominal segments have become generally considerably shorter. In some species (*buenoi, argenticollis, firmus, odontogaster*) this tendency is especially pronounced and the abdominal spiracles in these forms have shifted their positions to the middle of each segment. The ventral connexival sutures are reduced to two punctiform depressions in some species with more shortened abdominal segments. It should be noted that the abdominal spiracles are placed at the middle of each segment in two species of *Aquarius* with reduced abdominal segments (*G.* (*A.*) *remigis, G.* (*A.*) *ampla*).

Modifications of the other structures

The antennae: As noted under *Aquarius,* the length of the second segment in relation to the third has apparently become progressively smaller. In all species of *Gerris s. str.,* in which many structures especially the abdominal segments are more specialized, the second and third segments are subequal to each other as in some specialized species of *Aquarius.*

The rostrum: The third segment is less than three times as long as the last segment in all species and the proportional lengths of the two segments are quite constant in this subgenus. In *Aquarius* the relative length of the third to the fourth is evidently greater than in *Gerris s. str.* The relative length of the third to the fourth has apparently become smaller in the more specialized subgenus, *Gerris s. str.*

The subgenus *Gerris s. str.* is separated from *Aquarius* by the following characteristics:

(1) Different proportional lengths of the antennal segments.

(2) The hind tibia is about three times as long as its first tarsal segment, while it is over five times as long as its first tarsal segment in most species of *Aquarius.*

(3) The pronotum is without straight and carinated anterior margin in *Gerris s. str.*

(4) The connexival spine is much reduced or completely lost in *Gerris s. str.*

(5) The front leg has black mark instead of being wholly black as in *Aquarius.*

(6) There is evidence that the growth ratios for practically all antennal and leg segments are smaller than in *Aquarius.*

Subgenus *Limnoporus* Stål

(Figs. 14, 111, 223-233, 317-320)

Limnoporus Stål, Öfv. Vet. Akad. Förh., 27:395-396(1868) (as genus).
Limnoporus Puton, Synopsis Heter. Fr., 1:153(1879) (as genus).
Limnoporus Kirkaldy, Trans. Amer. Ent. Soc., 23:155(1906).
Limnoporus Kirkaldy and Torre-Bueno, Proc. Ent. Soc. Washington, 10:209 (1908) (as genus).
Limnoporus Torre-Bueno, Trans. Amer. Ent. Soc., 37:244(1911).
Limnoporus Bergroth, Proc. U. S. Nat. Mus., 51:237(1917) (as genus).
Limnoporus Van Duzee, Cat. Het., 1:428(1917) (as genus).
Limnoporus Poisson, Bull. Soc. Sci. Bretagne, 17(3-4):1-34(1940) (as genus).
Limnoporus Kiritschenko, Heteroptera of the European part of the Soviet Union, p. 100 (as genus).

Type species: *Gerris rufoscutellatus* Latreille, monobasic.

Species examined: *G.* (*L.*) *canaliculatus* Say, *G.* (*L.*) *dissortis*

Drake and Harris, *G. (L.) notabilis* Drake and Hottes, *G. (L.) rufoscutellatus* Latreille.

Color pattern: Pronotum with median longitudinal yellowish stripe extending onto posterior lobe.

Structures in wingless forms: Antenniferous tubercles long. Antenna slender, first segment always longest, but distinctly shorter than second and third ones together; third one shortest. Clypeus with basal margin distinct. Mandibular and maxillary plates clearly defined from each other. Rostrum long and slender, extending far beyond prosternum; third segment always over four times as long as last segment.

Pronotum slender, extending beyond posterior margin of mesonotum, anterior margin straight and carinated except for *canaliculatus,* posterior margin broadly rounded; uppersurface with a narrow, pale longitudinal carina throughout. Mesosternum a little over twice to two and a half times as long as metasternum; median longitudinal sulcus distinct in anterior half; paired longitudinal sutures distinct in anterior three fourths except for *canaliculatus* in which they are absent. Metanotum with median longitudinal sulcus distinct; metacetabular suture reaching well carinated lateral longitudinal suture of metanotum. Metasternum with omphalium located at about apical fifth of metasternum. Front leg slender; femur slightly dilated at apical third; tibia slightly swollen apically, without conspicuous process at inner apical angle; tarsus with first segment a little shorter than or subequal to second segment; claws arising from apical one fourth. Middle leg with *femur considerably shorter than hind femur,* about one and one fourth times as long as tibia; tibia a little less than twice as long as first tarsal segment; first tarsal segment under four times as long as second segment. *Hind leg about as long as middle leg* (only slightly shorter than middle leg); femur over one and a half times as long as tibia; tibia a little less than four times as long as first tarsal segment; first tarsal segment over twice as long as second tarsal segment.

Abdomen long, slightly dilated at middle. First tergite much shorter than second tergite, second to sixth tergite about as long as wide; seventh connexival segment always with conspicuous spine; second to seventh ventrites subequal in length to each other. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment. Ventral median longitudinal carina distinct; ventral connexival suture distinct, represented by discontinuous well impressed sutures on each segment.

Male: Seventh segment with ventral apical margin broadly concave. Eighth segment with ventral apical margin bisinuate or feebly produced at middle; ventral surface with or without median longitudinal elevation. Ninth segment with suranal plate simple; pygophore relatively small, rounded on apical margin; parameres reduced but distinctly recognizable. Endosoma with definitive dorsal plate roundly dilated on apical margin (part of apical plate), basally extends ventrad (fused basal plate); lateral plates rounded in apical regions; ventral lobe totally membranous and apically bifurcate in *dissortis,* more sclerotized and not bilobed in *canaliculatus;* apical region of endosoma not prolonged. (Description of the genitalia is based on *dissortis* and *canaliculatus*).

Female: Seventh segment ventrally slightly concave or feebly produced at middle on ventral apical margin. Eighth segment well exposed both dorsally and ventrally, both valvifers together narrowed apically and produced at middle or sinuate on apical margin, slightly elevated along inner margin of each valvifer (*canaliculatus*). First valvula with inner lobe split apically into two lobes, inner one of them membranous; outer lobe apically dilated, membranous and obtusely rounded. Second valvula with apex simply narrowed, folded on broadly rounded apical margin of intervalvular membrane; ramus slender but long. Vulva membranous, simply narrowed apically. (Description of the genitalia is based on *canaliculatus, dissortis,* and *notabilis*).

Modifications of the abdomen

(Figs. 317-320)

The male seventh segment: In *dissortis* and *notabilis* the seventh segment is considerably shorter than the sixth ventrally and has a more conspicuous connexival spine; in the other two species (figs. 317, 318) the seventh segment has become as long as sixth ventrally, accompanied by slight reduction of the connexival spine.

The male eighth segment: In *rufoscutellatus* (fig. 317) the apical half of the eighth ventrite is carinate on the median longitudinal axis and the apical margin is strongly produced. In *canaliculatus* (fig. 318) the eighth segment is elevated basally on the median longitudinal axis. In the other two more primitive species no conspicuous modification is apparent on the ventral surface.

The female seventh segment: The ventral apical margin of the seventh segment is simple and concave in all species except for *canaliculatus* (fig. 320) in which it is strongly produced at the middle. The degree of specialization as indicated by the relative lengths of the seventh and sixth segments is roughly in the following order from more primitive to more specialized: *notabilis, dissortis, rufoscutellatus, canaliculatus.* This order conforms well with that based on characters of the males. It should be also noted that in this genus, as in many other genera, the largest species is most primitive and the smallest one is most specialized as indicated by abdominal characters.

The subgenus *Limnoporus* is structurally close to *Aquarius* but can be distinguished by the following characteristics:

(1) Distinctly different proportional lengths of the antennal segments, *i. e.,* the first segment is shorter than the second and third together.

(2) The median longitudinal yellow stripe on the pronotum extends well onto the posterior lobe.

(3) The clypeus is more clearly defined basally.

(4) The hind femur is distinctly longer than middle femur; it is about as long as middle femur in *Aquarius* and also in *Gerris s. str.*

(5) The hind leg is only slightly shorter than the middle leg, while it is considerably shorter than middle leg in *Aquarius* and *Gerris s. str.*

(6) There is evidence that the growth patterns for at least the fourth antennal segments, the front and middle leg segments are probably significantly different from those in *Aquarius* and *Gerris s. str.*

Genus *Gerriselloides* Hungerford and Matsuda

(Figs. 9, 234-242)

Gerriselloides Hungerford and Matsuda, Ent. News, 69 (10):258-260(1958).
Gerris Horváth, Ann. Mus. Hung., 5:306(1907) (in part).

Type species: *Gerris brachynotus* Horváth, by original designation.

Species examined: *G. brachynotus* (Horváth).

Color pattern: Predominantly black dorsally. Head with a yellow crescent shaped spot at vertex. Pronotum with a median yellow stripe confined to anterior lobe; posterior lobe reddish brown. Meso- and metapleural regions with silvery pubescence. Abdominal tergites with a median elongate silvery spot on each segment.

Structures in wingless forms: Spindle shaped gerrids. Head wider than long including eyes. Eye with inner margin emarginated posteriorly, small, reaching posteriorly to anterolateral angle of pronotum, antenna short; first segment longest but shorter than second and third segments together; second and third segments subequal in length to each other; fourth segment much longer than third. Antenniferous tubercles well developed, about as long as eyes in dorsal view. Clypeus with basal margin well defined. Mandibular and maxillary plates distinct from each other. Rostrum short; third segment not extending beyond prosternum, about three times as long as last segment.

Pronotum fully prolonged, entirely covering mesonotum, *but relatively short, a little over twice as long as head;* anterior lobe with anterior margin nearly straight; posterior lobe a little longer than anterior lobe, defined from the latter by oblique suture coming from each side, slightly widened posteriorly and with a broadly rounded caudal margin, *with a dark sublateral longitudinal elevation;* uppersurface with a fine median longitudinal elevation tapering apically. Intersegmental suture between mesonotum and metanotum laterally continuous with metathoracic spiracle. Mesosternum relatively short, about twice as long as metasternum; median longitudinal sulcus distinct anteriorly; paired longitudinal sutures divergent posteriorly, distinct in anterior half of mesosternum. Metathoracic spiracle conspicuous. Metasternum with omphalium highly reduced; omphalial groove retained though lateral openings on metacetabula lost. Metanotum with lateral longitudinal elevations convergent anteriorly behind posterolateral angles of pronotum, without median longitudinal sulcus. Front leg with femur robust; tibia without apical thickening; tarsus with second segment longer than first segment and claws arising from near apex. Middle leg relatively stout; femur a little less than one and a half times as long as tibia; tibia twice as long as first tarsal segment; first tarsal segment a little over twice as long as second segment. Hind leg shorter than middle leg; femur a little less than twice as long as tibia; tibia over twice as long as first tarsal segment; tarsus relatively long, first segment twice as long as second segment.

Abdomen long, narrowed apically. First tergite with flattened W-shaped anterior margin, posterior margin elevated medially in male; second to fifth tergites subequal in length; sixth to seventh longer and narrower than the preceding segments; second to sixth ventrites subequal in length. Connexivum slightly reflexed; seventh segment without connexival spine in male, or slightly developed in female. Abdominal spiracles located closer to anterior margin than to posterior margin of each segment; ventral longitudinal suture of connexivum distinct throughout the entire length of each segment. Ventral median longitudinal elevation indistinct.

Male: Seventh segment longer than sixth ventrally, ventral apical margin simply concave. Eighth segment with ventral apical margin feebly concave. Ninth segment with suranal plate simple; pygophore with apical margin simply rounded. (Male genitalia were not dissected for study).

Female: Seventh segment longer than sixth ventrally; ventral apical margin slightly produced medially. Eighth segment with each valvifer depressed on surface. (Female genitalia were not studied).

Distribution: Eastern Siberia.

The genus *Gerriselloides* was originally assigned to *Gerris s. str.*, but it is different from the latter as follows:

(1) The clypeus has the basal margin distinct.

(2) The pronotum is short and with a sublateral longitudinal elevation.

(3) The mesosternum is relatively short. In a majority of species of *Gerris s. str.* the mesosternum is over two and a half times as long as the metasternum, while in this genus the mesosternum is only twice as long as the metasternum.

(4) The metasternum has retained the omphalial groove, although its lateral opening on the metacetabulum is lost.

(5) The metanotum is without median longitudinal sulcus.

(6) The ventral apical margin of the seventh abdominal segment of the male is simply concave; in a majority of species of *Gerris s. str.* the concave ventral apical margin of the same segment has a median smaller emargination.

(7) The ventral longitudinal suture of the connexivum is distinct as in *Aquarius.*

In spite of the above-mentioned differences, this genus is close to *Gerris s. str.* The lengths of the antennal and leg segments in relation to the body size are much as in *Gerris s. str.*, and roughly fall on the allometric growth slopes for those segments in *Gerris (Gerris) marginatus* Say.

Genus *Gerrisella* Poisson

(Figs. 10-11, 243-251)

Gerrisella Poisson, Bull. Hist. nat. Belg., 16(40):1-4(1940) (as subgenus of *Gerris*).

Gerrisella Hungerford and Matsuda, Florida Ent., 41(4); 165-168(1958) (as genus).

Type species: *Gerris settembrinoi* Poisson, by original designation.

Species examined: *Gerrisella settembrinoi* (Poisson).

Color pattern: Predominantly black. Eye reddish brown. Head with basal yellow mark. Pronotum with a broad median yellow stripe. Meso- and metapleural regions continuously grayish on either side of mesonotum and metanotum. Abdomen black. Basal half of legs yellow.

Structures in wingless forms: Female considerably larger than male. Head including eyes much wider than long, vertical region widened. Eye large, kidney-shaped, basal half of inner margin concave. Antenna slender. First segment strongly outcurved in apical half, about as long as second and third segments together, second to fourth segments subequal in length. Antenniferous tubercles slightly convergent anteriorly. Clypeus narrow, well defined at base. Mandibular and maxillary plates distinct from each other. Rostrum relatively long; third segment about three times as long as last segment.

Pronotum only feebly prolonged, its apical margin rounded, uppersurface longitudinally depressed in the middle. Intersegmental suture between mesonotum and metanotum obliterated laterally. Mesothorax strongly widened posteriorly. Mesosternum about four times as long as metasternum in male; median longitudinal sulcus recognizable only anteriorly. Metathoracic lateral longitudinal suture distinct, nearly reaching posterolateral margin of mesonotum, median longitudinal sulcus absent. Metasternum with distinct omphalium near posterior margin, without lateral groove of omphalium. Front leg without sexual difference in shape. Femur distinctly longer than tibia, somewhat curved and flattened at middle; tibia simply thickened apically; first tarsal segment greatly reduced; second segment with claws arising from apical fourth of second segment. Middle leg much longer than hind leg; femur a little longer and much more robust than tibia; first tarsal segment about three times as long as second tarsal segment, claws not recognized in the specimens examined. Hind leg with femur slender, a little longer than middle femur, about four times as long as tibia; first and second tarsal segment nearly equal in length.

Abdomen somewhat reduced in length. First segment (tergite) with flattened W-shaped anterior margin; second to seventh tergites with anterior margins feebly produced; first to sixth ventrites somewhat reduced in length; seventh segment with connexival spines absent. Abdominal spiracles from second to seventh located a little closer to anterior margin than to posterior margin of each segment; ventral margin of connexivum obscure.

Male: Seventh segment without median emargination on ventral apical margin. Eighth tergite greatly prolonged and broadly rounded on apical margin. Ninth segment with suranal plate provided with a ventrally directed process arising from apical region of each lateral margin; pygophore simply rounded on apical margin, elongate; parameres present.

Female: Not available for study.

Winged forms: Pronotum with anterior lobe well defined from posterior lobe, humeri located behind middle of pronotum. Hemelytra with Sc joined to R + M by oblique Sc_2 vein at the point of separation of R and M from basal R + M.

Distribution: Africa (Belgian Congo, Ivory Coast, Guinea).

This genus was formerly included in *Gerris,* but apparently is not closely related to it. This genus is more specialized than *Gerris s. str.* in the presence of the process on the lateral margin of the suranal plate, complete loss of the connexival spine of the seventh abdominal segment, great reduction of the pronotum in the wingless forms, etc. This genus, however, is more primitive than *Gerris s. str.* in the presence of the distinct basal margin of the clypeus, and distinctly differentiated mandibular and maxillary plates. As already found, the growth patterns for the antennal and leg segments are presumably considerably different from those in *Gerris s. str.* The location of the metathoracic spiracle is also different from that in *Gerris s. str.*

The phylogenetic position of this genus is obscure. It has possibly arisen as a distinct genus as a result of an independent specialization from a group ancestral to *Gerris* or *Limnogonus.*

Genus *Tenagogerris* Hungerford and Matsuda

(Figs. 12, 252-262)

Tenagogerris Hungerford and Matsuda, Ent. News, 59(9):225-229(1958).
Gerris Kirkaldy, Entomologist, 35:138(1902) (in part).
Gerris Hale, Ark. Zool., 17A(20):11(1925) (in part).
Gerris Lundblad, Arch. Hydrobiol., Suppl. 12, Tropische Binnengewässer, p. 370(1933) (in part).
Gerris Hungerford, Bull. Brooklyn Ent. Soc., 29:70(1934) (in part).

Type species: *Gerris euphrosyne* Kirkaldy, by original designation.

Species examined: *T. euphrosyne* (Kirkaldy).

Color pattern: Head and pronotum ferrugineous brown in ground color. Head with a broad black median longitudinal stripe and sublateral black stripes. Pronotum with a median longitudinal stripe which reaches posterior margin and with marginal black stripe, also with a pair of elongate black spots at anterolateral angles of pronotum which are continuous with marginal black stripe; propleural region with a broad black longitudinal stripe. The rest of body with dorsal surface black in ground color; mesopleural region largely clothed with short white pubescence on black ground color, thus giving a bluish tinge in certain lights, with a yellowish brown longitudinal stripe more ventrally. Body beneath paler.

Structures in wingless forms: Female much larger than male. Head including eyes wider than long. Eye strongly emarginated on inner margin. Antenna with first segment longest, but shorter than second and third segments together; second and third segments subequal in length, fourth a little longer than second and than third. Antenniferous tubercles shorter than eyes. Clypeus with basal margin indistinct but traceable. Mandibular and maxillary plates distinct from each other. Rostrum robust; third segment not extending beyond prosternum, about three times as long as fourth segment.

Pronotum fully prolonged, reaching a little beyond posterior margin of mesonotum, posterior margin broadly rounded; anterior and posterior lobes ill defined. Mesosternum a little over four times as long as metasternum, median longitudinal sulcus distinct only anteriorly; paired longitudinal sutures sometimes distinct in anterior third or half of mesosternum. Intersegmental suture between mesonotum and metanotum obliterated laterally. Metathoracic spiracle placed remotely from lateral margin of pronotum. Metanotum with lateral longitudinal suture well carinated, convergent anteriorly; median longitudinal sulcus of metanotum distinct. Metasternum with omphalium located near posterior margin; omphalial groove absent. Front leg slender; femur simple, without sexual difference; tibia simple, not dilated apically; tarsus with first segment shorter than second segment, claws arising from near apex of second segment. Middle leg slender; femur only slightly longer than tibia; tibia a little less than three times as long as first tarsal segment; first tarsal segment over four times as long as second. Hind leg shorter than middle leg; femur a little less than twice as long as tibia; tibia five times as long as first tarsal segment; first tarsal segment about twice as long as second segment.

Abdomen strongly narrowed posteriorly. First tergite with usual flattened W-shaped anterior margin, longer than second tergite;

second to fifth tergites subequal in length; seventh segment without connexival spine; ventrites more reduced than tergites. Abdominal spiracles placed a little closer to anterior margin than to posterior margin of each segment; ventral longitudinal margin of connexivum obliterated or represented by a shallow and obscure depression; ventral median longitudinal elevation distinct in female.

Male: Seventh segment much longer than sixth segment both dorsally and ventrally; ventral apical margin simply concave. Eighth segment with ventral apical margin concave. Ninth segment with suranal plate simple; pygophore with apical margin simply rounded; parameres vestigial. Endosoma with definitive dorsal plate with small apically rounded area; basal plate detached from base of dorsal plate, bearing largely membranous ventral plate apically; lateral plates slender and long, placed parallel to dorsal plate.

Female: Seventh segment about twice as long as sixth segment ventrally, ventral apical margin concave. Eighth segment with inner lobe of first valvula highly membranous and short; outer lobe sclerotized along both inner and outer margins except apex where is membranous and rather acutely narrowed apically. Second valvula sclerotized along outer margin, with membranous apical processes extending beyond apical margin of intervalvular membrane, which is with U-shaped dark area reaching apical margin; ramus slender. Vulva with broadly rounded apex and attached laterally to inner membranous lobe of first valvula.

Winged forms: Pronotum with humeri located behind middle, apical margin broadly rounded. Hemelytra with Sc joined to R + M near the point of branching into R and M.

Distribution: Australia.

This genus, at first glance, appears to be nothing but a *Tenagogonus.* Its general color pattern, the remote position of the metathoracic spiracle from the lateral margin of the pronotum, etc., suggest that this genus is a close relative of the *Limnometra-Tenagogonus* complex, but the relatively short and robust rostrum is exactly like *Gerris,* and the proportional lengths of the first three antennal segments are also more like *Gerris s. str.* than in *Tenagogonus.* In the species of the *Limnometra-Tenagogonus* complex of this size (8 to 10 mm.), the male is definitely longer than the female and the male apical abdominal segments are more or less conspicuously modified; while in this genus, which is represented by a single species, the female is definitely longer than the male, and the male apical abdominal segments are unmodified. This genus may possibly be the closest to the ancestral group of the Gerrini.

Genus *Eurygerris* Hungerford and Matsuda

(Figs. 5, 129, 263-287)

Eurygerris Hungerford and Matsuda, Florida Ent., 41(4):165-168(1958).
Gerris Champion, Biol. Centr. Amer., Rhynchota 2:147-149(1898) (in part).
Gerris Drake and Harris, Ann. Carnegie Mus., 23:179-240(1934) (in part).
Gerris Kuitert, Univ. Kansas Sci. Bull., 28(7):113-143(1942) (in part).
Brachymetra Berg, Com. Mus. Buenos Aires, 1:2(1898) (misidentification).

Type species: *Brachymetra fuscinervis* Berg, by original designation.

Species examined: *E. cariniventris* (Champion), *E. carmelus* (Drake and Harris), *E. flavolineatus* (Champion), *E. fuscinervis* (Berg), *E. kahli* (Drake and Harris), *E. mexicanus* (Champion), *E. summatus* (Drake and Harris).

Color pattern: Reddish brown in ground color in all species except for *flavolineatus,* in which it is nearly black. Head with a large black marking, basal pale yellow crescent-shaped marking well impressed. Pronotum in anterior lobe with pale yellow median longitudinal stripe. Silvery pubescent on the thorax. Abdomen and pronotum with at least anterior lobe black and with greenish tinge.

Structures in wingless forms: Male much smaller than female. Head including eyes about as long as wide. Eye elongate, inner margin strongly emarginated in posterior half. *Antenna without conspicuous difference in lengths among segments.* First segment always a little longer than second. Antenniferous tubercles feebly rounded on lateral margins. Clypeus with basal margin obliterated. Mandibular and maxillary plates sometimes indistinctly separated. Rostrum rather slender, slightly extending beyond prosternum; third segment from a little over three times to four times as long as last segment.

Pronotum prolonged in varying degrees in various species, reaching posterior margin of mesonotum in *mexicanus; transverse suture separating anterior lobe from posterior lobe well marked.* Intersegmental suture between mesonotum and metanotum distinct laterally. *Mesonotal region laterally more or less well carinated longitudinally and defined from mesopleural region.* Mesosternum with posterior margin feebly concave, about twice to a little over three times as long as metasternum in male; median longitudinal sulcus shallow or obscure; paired longitudinal sutures sometimes recognizable. Metathoracic spiracle located remotely from lateral margin of pronotum or of mesanotum. Metanotum with median longitudinal sulcus obliterated posteriorly; lateral longitudinal elevation not reaching mesonotum. Metasternum more or less conspicuously elevated on longitudinal axis in all species except for *flavolineatus* and *mexicanus;* omphalium highly vestigial, omphalial groove completely lost. Front leg with femur strongly curved and depressed on inner margin and with a protuberance at the apical end of depression in male; tibia slightly swollen apically, with a shallow longitudinal depression on inner margin near apex; first tarsal segment about as long as second segment; claws arising from near apex of second segment. Middle leg with femur a little longer than tibia; tibia apically curved in dried specimens, a little less than twice as long as first tarsal segment; first tarsal segment over five times as long as second in most species. Hind leg shorter than middle leg; femur a little longer than middle femur in most species; about twice as long as tibia in all species except for *mexicanus,* in which femur much less than twice as long as tibia; tibia about twice to three times as long as first tarsal segment; first tarsal segment twice to almost three times as long as second.

Abdomen more or less strongly narrowed posteriorly. First tergite with usual flattened W-shaped anterior margin, longer than second; second to sixth tergites and second to fifth ventrites subequal in length. Connexivum more or less strongly reflexed; connexival spine absent. Abdominal spiracles from second to sixth segments placed at middle of each segment except for female of *mexicanus,* in which they are placed closer to anterior margin than to posterior margin of each segment; those of seventh segment in female placed closer to anterior margin than to posterior margin. Median longitudinal carina present except for male of *mexicanus* and male and female of *flavolineatus.* Ventral longitudinal suture of connexivum represented by a dot-like depression on each segment in most species.

Male: Seventh segment with ventral apical margin with a shallow median emargination, longer than the preceding segment both dorsally and ventrally. Eighth segment strongly prolonged and cylindrical in some species; ventral apical margin emarginated. Ninth segment with suranal plate simply narrowed apically; pygophore rounded on apical margin; parameres vestigial. Endosoma with apical margin always strongly sclerotized, flat and broad; dorsal plate as in *Aquarius* and *Gerris s. str.,* basally appears to be fused with basal plate; ventral lobe membranous, broad and short; lateral plates short, almost indistinguishably fused with well sclerotized ventral basal region of endosoma in *mexicanus.* (Description of the genitalia is based on *mexicanus, fuscinervis,* and *carmelus.*)

Female: Seventh segment much longer than sixth in most species, telescoping eighth segment. Eighth segment apically exposed ventrally in most species. First valvula with well sclerotized inner lobe reaching middle of outer lobe; outer lobe thick, largely sclerotized, apex membranous and rounded, with a small spinous projection on inner apical angle. Second valvula with apex membranous, folded mesad, thus presenting a round apex; intervalvular membrane with apical margin mebranous, broadly rounded, feebly notched at middle. Vulva membranous, with a median apical production (Description of the genitalia is based on *fuscinervis, mexicanus,* and *cariniventris*).

Winged forms: Pronotum with humeri located at apical third, posterior margin broadly rounded. Hemelytra with Sc connected by Sc_2 with R + M basal to the point of separation of R and M from basal R + M, or with R near the point of separation.

Modifications of the abdomen

The male abdomen: The degree of specialization is seen in varying degrees of prolongation of the seventh to ninth segments. Six species, for which male specimens are available for study, can be arranged roughly in the following order from more primitive to more specialized on the basis of this feature.

mexicanus *flavolineatus*	The seventh segment is a little longer than either the sixth or the eighth ventrally.
cariniventris *kahli* *fuscinervis* *carmelus*	The eighth segment is longer than the seventh segment ventrally. In *carmelus* the seventh is about twice as long as sixth and the eighth is also about twice as long as the seventh and tubular in shape.

The female abdomen: In *mexicanus* and *flavolineatus* the seventh ventrite is a little less than twice as long as the sixth, but in *carmelus* the seventh is a little over twice as long as sixth at the middle, and laterally almost three times as long as the sixth due to prolongation of the posterolateral angle of the seventh connexival region. In the other four species the seventh segment is over twice as long as sixth. The spiracles of the third to fifth segments are located midway between the anterior and posterior margins of the segments except for *mexicanus* and *flavolineatus,* in which the pregenital abdominal segments are relatively long and the spiracles of the third, fourth and fifth segments are placed closer to the anterior margin than to posterior margin of each segment.

Modifications of the other structures

The pronotum: The pronotum in wingless forms is almost fully prolonged, reaching close to the posterior margin of the mesonotum in *mexicanus* (fig. 263); it reaches about the middle of the mesonotum in *carmelus, cariniventris, summatus, kahli,* and *fuscinervis* (fig. 264); it is only slightly prolonged and with a broad round margin in *flavolineatus* (fig. 265). The degree of reduction of the pronotum in wingless forms is thus least in *mexicanus* and highest in *flavolineatus,* although other structures have remained primitive in the latter species.

The front femur: In all species the front femur is more or less greatly depressed on the inner surface and the femur is greatly arched. In *mexicanus* and *flavolineatus* the inner surface is least depressed (figs. 282, 283), but in all others the inner surface is more strongly depressed and a low black protuberance exists near the apical end of the depression (figs. 284-287).

The hemelytra: The hemelytra with the vein Sc occasionally connected with R near the point of separation of R and M from the basal R + M by Sc_2 in *mexicanus;* in all other species the vein Sc is connected with R + M at various points basal to the point of separation of R and M, due to more distal separation of R and M.

This genus, though formerly included within the genus *Gerris,* cannot be the direct derivative of any one of more primitive subgenera of *Gerris.*

Genus *Limnogonus* Stål

(Figs. 7-8, 131, 151, 288-316, 321-334)

Limnogonus Stål, Hemip. Fabr., 1:132 (1866).
Limnogonus Kirkaldy and Torre-Bueno, Proc. Ent. Soc. Washington, 10:210 (1908).
Limnogonus Bueno, Trans. Amer. Ent. Soc., 37:244 (1911) (as subgenus of *Gerris*).
Limnogonus Bergroth, Proc. Nat. Mus., 51 (2150):237 (1917).
Limnogonus Lundblad, Arch. Hydrobiol. Suppl. 12, Tropische Binnengewässer, 4:374 (1933).
Limnogonus Drake and Harris, Ann. Carnegie Mus., 23:202-205 (1934).
Limnogonus Poisson, Bull. Soc. Sci. Bretagne, 17(3-4):12-13 (1940).
Limnogonus Kuitert, Univ. Kansas Sci. Bull., 17(3-4):125 (1942).
Limnogonus Hungerford, Proc. 10th Intern. Congr. Ent., pp. 344, 346 (1858).
Limnogonus Hungerford and Matsuda, Jour. Kansas Ent. Soc., 32(1):40-41 (1959) (described *Limnogonellus*).
Lamprotrechus Reuter, Öfv. Finska Vet. Soc. Förh., 25:40 (1882) (as subgenus of *Gerris,* type species, *Gerris leptocerus* Reuter).
Tenagogonus Van Duzee, Cat. Hemip., 249 (1917) (misidentification).

Type species: *Hydrometra hyalina* Fabricius, by subsequent designation (Drake and Harris 1934, in the above reference).

Species examined: *L. (Limnogonus) aduncus* Drake and Harris, *L. (Limnogonus) australis* (Skuse), *L. (Limnogonus)* buxtoni Esaki, *L. (Limnogonus) darthulus* Kirkaldy, *L. (Limnogonus) fossarum* (Fabricius), *L. (Limnogonus) guerini* (Lethierry et Severin), *L. (Limnogonus) hyalinus* (Fabricius), *L. (Limnogonus) hypoleucus* (Gerstaecker), *L. (Limnogonus) ignotus* Drake and Harris, *L. (Limnogonus) intermedius* Poisson, *L. (Limnogonus) cereiventris leptocerus* (Reuter), *L. (Limnogonus) luctuosus* (Montrouzier), *L. (Limnogonus) lundbladi* Usinger, *L. (Limnogonus) nitidus* (Mayr), *L. (Limnogonus) profugus* Drake and Harris, *L. (Limnogonus) recens* Drake and Harris, *L. (Limnogonus) recurvus* Drake and Harris, *L. (Limnogonellus) celeris* Drake and Harris, *L. (Limnogonellus) hesione* (Kirkaldy), *L. (Limnogonellus) lotus* B.-White, *L. (Limnogonellus) lubricus* B.-White, *L. (Limnogonellus) parvulus* (Stål), *L. (Limnogonellus) visendus* Drake and Harris.

Color pattern: Uppersurface predominantly black, lustrous in most species. Head typically with a pair of yellow sublateral longitudinal stripes. Pronotum typically with a median longitudinal yellow stripe either reaching or not reaching posterior margin, and with a pair of elongate yellowish spots on either side of the median longitudinal yellow stripe; in *Limnogonellus* the yellow longitudinal stripe is replaced by a yellow spot. Mesothorax typically with a silvery longitudinal stripe. Tergites with a continuous yellow longitudinal stripe in many species.

Structures in wingless forms: Head including eyes wider than long. Eye with inner margin strongly emarginated. Antenna slender, much shorter than length of body. First segment two thirds to three fourths as long as second and third together in most species; third segment as long as or a little shorter than second; fourth segment much longer than third in most species. Antenniferous tubercles shorter than eyes. Clypeus with basal margin not very distinct. Mandibular and maxillary plates indistinctly separated. Rostrum rather slender and long; third segment about two and a half times to about four times as long as last segment.

Pronotum fully prolonged and covering mesonotum in most species; anterior lobe with a pair of obscure depressions; posterior lobe occasionally faintly longitudinally carinate in the middle. Intersegmental suture between mesonotum and metanotum lost laterally. Mesosternum three to five times as long as metasternum;

median longitudinal sulcus distinct anteriorly; paired longitudinal sutures distinct in some species. Metathoracic spiracle placed at some distance from pronotum. Metanotum with lateral elevations well marked and convergent anteriorly; median longitudinal sulcus distinct in some species. Metasternum with omphalium present; omphalial groove absent. Front leg with femur a little longer than tibia, curved in basal third in some species; tibia slender, without conspicuous process; tarsus with first segment about as long as second to less than half as long as second. Middle leg with femur always a little longer than tibia; tibia about twice to three times as long as first tarsal segment; first tarsal three to five and one third times as long as second segment. Hind leg shorter than middle leg; femur two and a half times to a little less than one and a half times as long as tibia; tibia three to six times as long as first tarsal segment; first tarsal segment one and a half to a little less than two and a half times as long as second.

Abdomen narrowed posteriorly. First tergite with anterior margin W-shaped, as long as second tergite in most species; second to fifth tergites subequal in lengths; ventrites more reduced. Connexivum with or without connexival spine. Abdominal spiracles placed at middle between anterior and posterior margins of each segment; ventral margin of connexivum represented by two dot like depressions on each segment; ventral median longitudinal elevation or suture obscure or lost.

Male: Seventh segment simply concave and without smaller median emargination on ventral apical margin. Eighth segment with ventral apical margin simply concave or with a median production of various shapes in some species. Ninth segment with suranal plate narrowed apically in distal half; pygphore broadly rounded on apical margin; parameres vestigial or absent. Endosoma in species from the Western Hemisphere highly uniform (*aduncus, guerini, recens, profugus, hyalinus, ignotus, recurvus*), always well developed and sclerotized apically; definitive dorsal plate on apical margin bifurcate and directed cephalad apically; ventral lobe always slender and relatively long, sclerotized at least basally. In species from the Eastern Hemisphere *(fossarum, cereiventris, hypoleucus, australis, nitidus*) structural patterns are widely different from each other; basal plate fused to dorsal plate in most species. In *Limnogonellus (lubricus, visendus, hesione)* endosoma is also widely different in shape. In *lubricus* endosoma is without apical prolongation and ventral plate totally membranous; in *visendus* endosoma abnormally prolonged and well sclerotized apically; in *hesione* lateral plate long etc. (Description of the genitalia is based on the species mentioned in the above description).

Female: Seventh segment always longer than sixth ventrally; connexivum with spine rather conspicuous in some species, or strongly reduced in some species; ventral apical margin simply concave or produced medially in some species. Eighth segment basally telescoped within tubular seventh segment. First valvula not well sclerotized, with well differentiated inner lobe reaching middle of outer lobe, or inner lobe lacking; outer lobe narrowed apically, with short dark hairs scattered over surface of apical half. Second valvulae membranous, with short dark hairs scattered in apical half, apex acute or broadly rounded, directed mesad beyond apical margin of intervalvular membrane. (Description of the genitalia is based on *aduncus, recurvus, guerini, hyalinus, hesione,* and *visendus*).

Winged form: Pronotum with humeri located behind middle, apex subacute in most species. Hemelytra as in *Gerris.* Sc is connected with R + M at the point of separation into R and M.

Distribution: World-wide. The subgenus *Limnogonellus* occurs both in the Eastern and Western Hemispheres.

Subgenus *Limnogonus* Stål, *s. str.*

For type designation and citations see generic bibliography.

Color pattern: Pronotum with a median longitudinal yellow stripe either reaching or not reaching posteror margin, and with a pair of elongate yellow spots or short stripes on either side of median longitudinal stripe.

Structures in wingless forms: Fourth antennal segment much longer than third segment. Pronotum fully prolonged. Middle tibia a little over twice as long as first tarsal segment in most species; first tarsal segment a little over four times as long as second. Hind leg with tibia over half as long as femur. Abdomen with male eighth abdominal segment prolonged and modified on ventral apical margin in many species.

Subgenus *Limnogonellus* Hungerford and Matsuda

Limnogonellus Hungerford and Matsuda, Jour. Kansas Ent. Soc., 32(1):40-41 (1959) (as subgenus of *Limnogonus*).

Type species: *Gerris parvula* Stål, by original designation.

Structures in wingless forms: Fourth antennal segment about as long as or shorter than third in majority of species. Pronotum not fully prolonged in most species. Middle tibia much over twice as long as first tarsal segment in majority of species. Hind leg with tibia about half or less than half as long as first tarsal segment. Abdomen with male eighth abdominal segment neither prolonged nor modified ventrally.

Besides the above mentioned distinctions between the two subgenera we have already observed indications that the growth patterns at least for the fourth antennal segment in *Limnogonellus* are significantly different from those in *Limnogonus s. str.*

In an African species, *Limnogonus intermedius* Poisson, there is strong indication that the growth patterns for all antennal and leg segments are presumably greatly different from those in any subgenus of *Limnogonus.* In this species the color patterns of the head, pronotum, mesopleuron, and abdomen are also considerably different from those in typical *Limnogonus* species. This species, together with a few other African species, probably represent a distinct genus.

Modifications of the abdomen

(Figs. 302-316)

The male seventh segment: The degree of specialization of the segment as indicated by the relative lengths of the seventh and sixth can be roughly arranged in the following order: *nitidus, cereiventris lepocerus, darthulus, guerini, australis, ignotus, aduncus, luctuousus, recens, profugus, buxtoni, hyalinus, recurvus, visendus, lotus, lubricus, celeris, parvulus, hesione, lundbladi.* It can well be said that *Limnogonellus,* which is shorter in body length, is more specialized than *Limnogonus s. str.* in this respect. The relative lengths of the seventh to the sixth ranges from 10:9 in *nitidus* to 3:10 in *lundbladi.* A conspicuous connexival spine occurs only in *nitidus* and *hypoleucus;* in all other species the spine has been more or less greatly reduced or is completely lost.

The male eighth segment: The specialization of the eighth segment is indicated by the prolongation of the segment itself and the modification of the ventral apical margin. In *nitidus, hypoleucus, ignotus, cereiventris, guerini, leptocerus, buxtoni, darthulus* and *profugus* the eighth segment is relatively short (exception *profugus*) and the ventral apical margin is simply concave. In *fossarum* and *luctuosus* the eighth segment is more or less prolonged and the ventral apical margin is produced at the middle but not modified into conspicuous process. In *aduncus, hyalinus, recens* and *lundbladi* the eighth segment is prolonged and the ventral apical margin is provided with a conspicuous process of various shapes at the middle. In *parvulus, celeris, visendus, hesione, lotus,* which belong to the subgenus *Limnogonellus,* the segment is not prolonged and the ventral apical margin is simply concave although the seventh segment in this subgenus is greatly prolonged.

The male ninth segment: The ninth segment has remained relatively simple in this genus. The pygophore is always simply rounded on the apical margin. In some species, in which the seventh and eighth segments are specialized, the pygophore is also somewhat prolonged. In *hyalinus* the pygophore is covered with a mass of long hairs laterally and in *lundbladi* it is large and with a lateral depression on each side. The suranal plate is simple in all species except for *visendus,* in which the middle area is strongly dilated and clothed with a conspicuous tuft of hairs.

The female seventh segment: The relative lengths of the sixth and the seventh ventrites are from 18:21 in *cereiventris leptocerus,* 17:21 in *nitidus,* 14:28 in *recens,* 15:33 in *hyalinus* to 3:10 in *lundbladi.* In the more primitive species such as *nitidus, hypoleucus* and *cereiventris leptocerus* the connexival spine is conspicuous or at least clearly recognizable and the ventral apical margin of the seventh ventrite is simply broadly concave. In *fossarum, buxtoni, australis, recens, recurvus, hyalinus,* etc., the segment is prolonged and the ventral apical margin is more or less bisinuate with a median projection and the connexival spine is rather inconspicuous or nearly absent. The highest degree of prolongation of the seventh ventrite is noted in *lundbladi* as seen from figure 316. In *Limnogonellus* including *visendus, lubricus, parvulus, hesione, celeris* and *lotus,* the relative lengths of the sixth and seventh segments are about as 1:2, the connexival spine is obsolete except for *visendus,* and the apical margin of the ventrite is slightly produced at the middle except for *lotus,* in which it is simply concave.

It is noted from the foregoing discussion that the subgenus *Limnogonellus* appears to exhibit a trend in the eighth (male) and seventh (female) segments somewhat different from *Limnogonus s. str.*

Genus *Tachygerris* Drake

(Figs. 2, 112, 132, 150, 335-358)

Tachygerris Drake, Proc. Biol. Soc. Washington, 70:193 (1957).
Tachygerris Hungerford and Matsuda, Jour. Kansas Ent. Soc., 31 (2):113-115 (1958).
Limnometra Champion, Biol. Centr. Amer., Rhynch., 2:150-151 (1898) (in part).
Tenagogonus Kuitert, Univ. Kansas Sci. Bull., 28 (7):131-135 (1942) (in part).

Tachygonus Drake, Proc. Biol. Soc. Washington, 70:111 (1957) (preoccupied, type species, *Tenagogonus adamsoni* Drake).

Type species: *Tenagogonus adamsoni* Drake, by original designation.

Species examined: *T. celocis* (Drake and Harris), *T. adamsoni* (Drake), *T. opacus* (Champion), *T. quadrilineatus* (Champion), *T. spinulatus* (Kuitert), *T. surinamensis* Hungerford and Matsuda.

Color pattern: Predominantly reddish brown. Head with a median pair of black stripes confluent posteriorly, lateral pair of black to fuscous stripes are along inner margin of eyes. Pronotum with a median and lateral pair of black stripes which together tend to be confluent in posterior half of pronotum. Mesopleural region usually with two rather faint fuscous stripes, and white between them. Hemelytra dark fuscous, scattered with short golden hairs. Body beneath paler. Silvery pubescent on mesocoxa and metacoxa. General color pattern somewhat similar to that in *Onychotrechus* and *Amemboa.*

Structures in winged forms: Always winged. Head including eyes wider than long. Eye elongate but large, inner margin strongly emarginated posteriorly. Antenna slender but shorter than body; first segment curved, thicker than the rest, apex truncate, shorter than third; second segment always shortest; third segment twice or little less than twice as long as second; fourth segment longest. Antenniferous tubercle acute at tip, rounded on lateral margin. Clypeus with basal margin indistinct. Mandibular and maxillary plates clearly separated. Rostrum long, reaching mesosternum; first segment well developed, about half as long as head; third segment three to four times as long as fourth.

Pronotum long, simply gradually widened in anterior two thirds, then narrowed posteriorly ending in rather narrowly rounded apical margin. Hemelytra with Sc connected with R + M by Sc_2 before the point of separation of R and M from basal R + M. Primary intersegmental suture between mesonotum and metanotum distinct laterally between metathoracic spiracle and wing base. Mesosternum three and a half to four times as long as metasternum; paired longitudinal sutures absent; median longitudinal sulcus distinct anteriorly. Metanotum with median longitudinal sulcus distinct, lateral longitudinal elevation extending anteriorly nearly to hind wing base; metacetabular suture obliterated dorsally. Metasternum about twice as long as definitive first abdominal ventrite; omphalium located on median longitudinal elevation at apical third, posterior margin feebly concave. Front leg long. Femur longer than tibia, more curved and slightly dorsoventrally flattened basally; tarsus with first segment subequal to second in length, claws small, arising preapically. Middle leg with femur one and one third as long as tibia in most species; tibia about one and a half times as long as tarsus; first tarsal segment about six times as long as second, claws arising from near apex. Hind leg shorter than middle leg; femur over twice as long as tibia; tibia between three and four times as long as first tarsal segment; first tarsal segment twice or a little over twice as long as second, claws slender, arising from near apex.

Abdomen long. First tergite with flattened W-shaped anterior margin. Pregenital ventrites subequal in length; seventh segment with connexival spines inconspicuous or absent. Abdominal spiracles placed at middle of segments. Ventral longitudinal margin of connexivum clearly recognizable, especially in females. Ventral median longitudinal elevation present in some species.

Male: Seventh segment with ventral apical margin simply concave, without distinct connexival spines. Eighth segment with ventral apical margin shallowly concave. Ninth segment with suranal plate widened at middle; pygophore ventrally well exposed, simply rounded on apical margin; parameres vestigial. Endosoma with definitive dorsal plate (dorsal plate + basal plate) reaching basal half of dorsal margin of endosoma, extending posteriorly along basal margin; membranous ventral plate reaching apex of endosoma; apical plate apparently lost; lateral plates slender and simple. (Description of male genitalia is based on *spinulatus, celocis, quadrilineatus.*)

Female: Seventh segment ventrally well developed, variously modified in various species, connexival spines inconspicuous. Eighth segment ventrally completely concealed by seventh ventrite; first valvula highly reduced, inner lobe short and acutely pointed, lateral lobe short and connected by ramus with outer margin of process of ninth tergite (in figure 352 the ramus appears to be attached on inner margin, but this is actually outer margin. The lobe is twisted around laterally in the figure). Second valvula with lateral lobe far extending beyond apical margin of intervalvular membrane which is broadly rounded. (Description of female genitalia is based on *opacus.*)

Distribution: Central and South America (Bolivia, Brazil, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Paraguay, Peru, Surinam).

The genus *Tachygerris* is peculiar in the following characteristics:

(1) The wingless form has never been found.

(2) The omphalium is located on the longitudinal elevation.

(3) The vein Sc is connected with R + M at a point basal to the point of separation of R and M from R+M.

(4) The second antennal segment is shortest.

(5) The seventh abdominal segment of the female has the ventral apical margin more or less greatly modified in various shapes in different species.

(6) The female genitalia have the first and second valvulae greatly reduced.

(7) The apical segment of the endosoma has the dorsal plate reaching only to the middle of dorsal margin of endosoma.

(8) The growth slopes for the first three antennal segments are probably very steep.

(9) The growth slopes for the leg segments are also probably steeper than in other genera of the tribe.

Modifications of the abdomen in *Tachygerris*

The male: The degree of specialization of the seventh segment, as indicated by its length in relation to the sixth, indicates an order, from more primitive to specialized as follows: *quadrilineatus, spinulatus, celocis, adamsoni, opacus.* There is no conspicuous modification on the ventral surface of the eighth segment in any species of the genus. In *quadrilineatus* and *duolineatus* the eighth segment is quite short, thus presumably most primitive; in the other species the segment is considerably more prolonged.

The female: The connexival spine is more developed in *duolineatus* than in the other species. The ventral apical margin is variously modified in the species and is of taxonomic importance at the species level (figs. 346-351).

Genus *Tenagogonus* Stål

(Figs. 4, 6, 16, 127, 130, 149, 359-415)

As has been revealed in the study by Hungerford and Matsuda (1858), *Limnometra* and *Tenagogonus,* though treated as distinct genera, actually constitute a large natural group. To express this relationship and yet maintain *Tenagogonus* and *Limnometra* as entities, Doctor Hungerford and I now think that these groups can be best regarded as subgenera. *Tenagometra* Poisson also belongs to this genus.

Type species: *Tenagogonus albovittatus* Stål, first included species.

Species examined: *T. (T.) albovittatus* Stål, *T. (T.) brevis* (Lundblad), *T. (T.) divergens* Hungerford and Matsuda, *T. (T.) dubius* Poisson, *T. (T.) fijiensis* Hungerford and Matsuda, *T. (T.) kuiterti* Hungerford and Matsuda, *T. (T.) madagascariensis* Hoberlandt, *T. (T.) pravipes bergrothi* Hungerford and Matsuda, *T. (T.) robustus* Hungerford and Matsuda, *T. (T.) zambezinus* (Poisson), *T. (L.) anadyomene* (Kirkaldy), *T. (L.) annulicornis* (Breddin), *T. (L.) borneensis* (Hungerford and Matsuda), *T. (L.) ciliatus* (Mayr), *T. (L.) cursitans* (Fabricius), *T. (L.) femoratus* (Mayr), *T. (L.) fluviorum* (Fabricius), *T. (L.) inermis* (Mayr), *T. (L.) insularis* (Hungerford and Matsuda), *T. (L.) kallisto* (Kirkaldy), *T. (L.) minutus* (Mayr), *T. (L.) nigripennis* (Mayr), *T. (L.) octopunctatus* (Hungerford), *T. (L.) palauanus* (Esaki), *T. (L.) pulchrus* (Mayr), *T. (L.) rossi* (Hungerford and Matsuda), *T. (L.) vulpinus* (Breddin), *T. (Tenagometra)* sp.

Color pattern: Reddish brown to yellowish brown in general coloration. Head always with a pair of lateral and a pair of median black longitudinal stripes which are confluent anteriorly, median pair often represented by a single median black longitudinal stripe. Pronotum always with black marginal stripe and a median longitudinal stripe which usually extends entire longitudinal axis of pronotum, anterior lobe occasionally provided with a pair of black markings on either side of middle. Mesothorax with two black longitudinal stripes which may or may not be confluent posteriorly. Undersurface paler.

Structures in wingless forms: Head including eyes wider than long. Eye strongly emarginated in posterior half of inner margin. Antenna slender, often as long as or longer than length of body; proportional length of second segment to first greater in male than in female; first segment longer than or at least as long as second; second segment more often longer than third segment than vice versa; fourth segment longest except for *ciliatus, cursitans* and *Tenagometra.* Antenniferous tubercles short. Clypeus with basal margin distinct in most species, widened posteriorly. Mandibular and maxillary plates at least distinguishable from each other in most species. Rostrum reaching anterior third of mesosternum in most species; first segment relatively long, about half as long as head; third segment three to five times as long as last segment.

Pronotum fully prolonged to cover mesonotum except for *mada-*

gascariensis and *Tenagometra,* slightly dilated in apical fourth, occasionally apical region modified into a narrow process *(fijiensis).* Intersegmental suture between mesonotum and metanotum indistinct laterally. Mesosternum three to six and a half times as long as metasternum; median longitudinal sulcus present at least in anterior half; paired longitudinal sutures retained in more primitive species of *Limnometra* (*femoratus,* etc.). Mesonotum with median longitudinal sulcus distinct throughout; lateral longitudinal elevation distinct. Metathoracic spiracle located at some distance from lateral margin of pronotum. Metasternum with omphalium represented by small tubercle placed close to apical margin of metasternum (position of omphalium somewhat varies in various species); omphalial groove absent. Front leg relatively long, longer than length of body in some specialized species of *Tenagogonus s. str.*; femur subequal in thickness throughout; tibia slightly thickened at apex, distinctly constricted near apex, with a shallow longitudinal depression on inner margin near apex, without conspicuous process at inner apical angle; proportional length of first tarsal segment to second segment varies in various species, but never less than half as long as second; claws arising from near apex, with a short membranous arolium. Middle leg with femur a little longer than tibia in some species, less than one and one fourth as long as tibia in most species; tibia twice to four times as long as first tarsal segment in most species, seldom over four times as long as first tarsal segment *(nigripennis)*; first tarsal segment three and one fourth to seven times as long as second tarsal segment; second segment with claws arising from near apex; middle femur and tibia ventrally ciliated in some species *(ciliatus, femoratus).* Hind leg shorter than middle leg; femur as long as to a little over twice as long as tibia; tibia always about five times as long as first tarsal segment; first tarsal segment a little over three times to one and two seventh times as long as second segment; second segment with small claws arising from near apex.

Abdomen varies greatly in length. In some more primitive species of *Limnometra* pregenital segments are subequal in length to each other; in some more specialized species of *Tenagogonus* pregenital segments are highly reduced. First tergite with usual flattened W-shaped anterior margin. Abdominal spiracles placed closer to anterior margin than to posterior margin in majority of species of *Limnometra* and *Tenagometra,* or placed at middle of each segment in all species of *Tenagogonus;* ventral connexival suture not very distinct, represented by a dot like depression or obscure in specialized species; ventral median longitudinal carina distinct in most species of *Limnometra.*

Male: Seventh segment with connexival spine in more primitive species, absent in more specialized species; ventral apical margin simply concave, or with paired processes of various shapes, ventral surface also modified in some species. Eighth segment with ventral apical margin simply concave in most species, modified in some species *(madagascariensis, robustus).* Ninth segment with suranal plate simple in all species; pygophore simply narrowed apically, surface modified and lateral margin with a conspicuous mass of black hairs in *madagascariensis;* parameres highly reduced. Endosoma without apical prolongation in more specialized species; dorsal plate bifurcate apically, basally articulated with basal plate; ventral lobes always bilobed and more sclerotized in some species, supported basally by basal plate; lateral plates simple and long; proximal segment of endosoma strongly sclerotized *(albovittatus)* or with paired ventral processes and smaller lateral processes arising from lateral apical margin *(madagascariensis).* (Description of the genitalia is based on *ciliatus, cursitans, femorata, madagascariensis, albovittatus.)*

Female: Seventh segment with or without conspicuous connexival spine; ventral apical margin concave or prolonged medially covering eighth segment above in some species. Eighth segment ventrally exposed in some species; first valvula with inner lobe loosely attached to outer lobe; outer lobe simply narrowed, or shorter and rounded apically. Second valvula apically directed mesad from each side, far extending beyond apical margin of intervalvular membrane which is straight (in *albovittatus* inner apical margin subhorizontally continuous); ramus short in more specialized species. (Description of the genitalia is based on *ciliatus, femoratus, pravipes bergrothi, madagascariensis* and *albovittatus*).

Winged forms: Sc connected with R + M at the point of separation into R and M. Pronotum with humeri located at apical third or a little behind middle.

Distribution: Oriental region (Borneo, Burma, Ceylon, India, Java, Malaya, Philippines, Sumatra, Thailand), Australian region (Australia, Fiji, Moluccas, New Guinea, Palau Island, Solomon Islands), and Ethiopian region (Belgian Congo, Gabon, Madagascar, Natal, Rhodesia, South Africa, Tanganyika, West Africa, Zululand). Only one species included in the subgenus *Limnometra* is known from Africa.

Subgenus *Limnometra* Mayr

Limnometra Mayr, Verh. Zool.-Bot. Vereins, Wien, 15:443 (1865) (as genus).
Limnometra Bergroth, Zool. Med. Mus. Nat. Hist. Leiden, 1(2):121-123 (1915) (*Limnometra* as synonym of *Tenagogonus*).
Limnometra Lundblad, Arch. Hydrobiol. Suppl. 12, Tropische Binnengewässer, 4:388-392 (1933) (*Limnometra* as a distinct genus).
Limnometra Hungerford and Matsuda, Univ. Kansas Sci. Bull., 39(9):371-457 (1958) (*Limnometra* as genus).

Type species: *Limnometra femorata* Mayr, by original designation.

Body relatively long. Length of second relative to first antennal segment greater in male than in female. Pronotum fully prolonged in wingless forms. Abdomen long. Connexival spine present. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment in most species. Male seventh and eighth segments not greatly modified.

Subgenus *Tenagogonus* Stål *s. str.*

Tenagogonus Stål, Öfv. K. Vet. Akad. Förh., 10:263 (1853) (no species described).
Tenagogonus Stål, Öfv. K. Vet. Akad. Förh., 12:45 (1855) (*T. albovittatus* described).
Tenagogonus Bergroth, Zool. Med. Mus. Nat. Hist., Leiden, 1(2):121-123 (1915) (*Limnometra* as a synonym of *Tenagogonus*).
Tenagogonus Lundblad, Arch. Hydrobiol. Suppl. 12, Tropische Binnengewässer, 4:388-392 (1933) (*Tenagogonus s. str.* as a genus).
Tenagogonus Hungerford and Matsuda, Univ. Kansas Sci. Bull., 39(9):371-457 (1958) (*Tenagogonus s. str.* as a genus).
Tenagogonellus Poisson, Mem. Inst. Sci. Madagascar A, 1(2):94 (as a subgenus of *Tenagogonus,* type species, *Tenagogonus madagascariensis* Hoberlandt).

Type species: *Tenagogonus albovittatus* Stål, first included species.

Body relatively short. Length of second relative to first antennal segment greater in male than in female. Pronotum fully prolonged in wingless forms of most species. Abdomen relatively short. Connexival spine absent in most species. Abdominal spiracles placed at middle of abdominal segments. Male seventh and eighth abdominal segments more or less greatly modified.

Modification of the abdomen

(Figs. 388-406)

The male seventh segment: In *T. (L.) ciliatus, T. (L.) cursitans, T. (L.) femoratus, T. (L.) nigripennis, T. (L.) pulchrus, T. (L.) annulicornis, T. (L.) kallisto, T. (L.) lipovskyi, T. (L.) fluviorum, T. (L.) borneensis, T. (L.) rossi* the seventh segment is shorter than or nearly equal to the sixth and the connexival spine is more or less conspicuous, surpassing the tip of the abdomen in many species; *T. (L.) lipovskyi* (fig. 398) is the only exception, and in this species the connexival spine is almost completely lost. In these species the second to sixth ventrites are long, more or less subequal in length, and the mesosternum is never more than four times as long as metasternum.

In *T. (L.) anadyomene* (fig. 389), *T. (L.) palauanus, T. (L.) octopunctatus* (fig. 397), *T. (T.) kuiterti* (fig. 399) the seventh ventrite is longer than the sixth, and the connexival spine has become less conspicuous, never surpassing the tip of the abdomen; in *T. (T.) kuiterti* the connexival spine is completely lost. In these species the mesosternum is about four times as long as the metasternum or even much over four times as long as metasternum in *T. (T.) kuiterti*; the first to sixth segments are shorter than in the preceding groups of species and the segments have become increasingly unequal in length to each other. The abdominal spiracles have shifted their positions to the middle of each segment in *T. (L.) anadyomene* and *T. (T.) kuiterti*.

Accompanied by further reduction of the metasternum and the first to sixth abdominal segments, *T. (T.) kampaspe* (fig. 395), *T. (T.) robustus* (fig. 402), *T. (T.) divergens* (fig. 392), *T. (T.) fijiensis, T. (T.) pravipes bergrothi, T. (T.) madagascariensis* (fig. 393, 401), *T. (T.) albovittatus* (fig. 400), *T. (T.) zambezinus* (fig. 391) exhibit paired processes on the ventral apical margin of the seventh segment except for *T. (T.) robustus, T. (T.) pravipes bergrothi*, and *T. (T.) fijiensis*. The processes arise on different parts of the ventrolateral margin in different species, from near the posterolateral angle of the seventh connexival segment almost to the ventral longitudinal axis of the abdomen. It is interesting to observe the sequence of reduction of the connexival spine and the concomittal development of the processes on the ventrolateral margin (figs. 391-395). In the last group of species the abdominal spiracles of the second to sixth segments are in the middle of each segment.

The male eighth abdominal segment: The modification of the eighth segment is also correlated with reduction of the first to sixth abdominal segments. Among the species with more primitive pregenital segments (first to sixth) the eighth ventrite has remained unmodified in most species. In *T. (L.) ciliatus* and *T. (L.) octopunctatus* (fig. 397), however, a small projection has arisen on the posterior margin laterally, and in *T. (L.) lipovskyi* (fig. 398) paired processes have arisen on the basal lateral area of the eighth ventrite. Among the species with more specialized abdomens a triangular notch occurs at the middle of apical margin of the eighth ventrite in *robustus* (fig. 402) and a pair of slender processes occurs on the apical margin in *T. (T.) madagascariensis* (fig. 401).

The male ninth segment: The suranal plate has remained simple except in *T. (T.) albovittatus,* in which a pair of slender, black processes arises from the middle of lower margin. The pygophore is modified in a highly specialized species, *T. (T.) madagascariensis* (fig. 401), in which it is strongly widened medially and provided with a conspicuous tuft of thick, black hairs on the upper margin at the middle. The endosoma has the proximal segment simply membranous in primitive species, but in *T. madagascariensis* the proximal segment is provided with ventral apical processes and with a lateral subtriangular process; in *T. (T.) albovittatus* the proximal segment is strongly sclerotized.

The female abdomen: The degree of specialization of the female in this group of gerrids is also indicated by loss of uniformity in the lengths of abdominal segments, accompanied by prolongation, especially of the sixth and seventh segments. In most species with more primitive abdomens, such as *T. (L.) ciliatus* (fig. 403), *T. (L.) femoratus, T. (L.) palauanus, T. (L.) borneensis, T. (L.) nigripennis, T. (L.) pulchrus, T. (L.) cursitans, T. (L.) annulicornis,* and *T. (L.) kallisto,* the seventh segment is shorter than the sixth, its apical margin is simply concave, and the connexival spine is always conspicuous. In *T. (L.) octopunctatus* (fig. 404), *T. (L.) rossi, T. (L.) lipovskyi,* and *T. (L.) anadyomene* the seventh segment is considerably longer than the sixth except for *T. (L.) lipovskyi;* the connexival spine is less conspicuous and never surpasses the tip of the abdomen. In the rest of the species the seventh segment is much longer than the sixth, and the connexival spine has become inconspicuous or is totally lost as noted in *T. (T.) kampaspe* and *T. (T.) fijiensis* (fig. 406), in which the apical margin of the seventh ventrite is produced medially. The highest degree of prolongation of the seventh segment is attained also in *T. (T.) fijiensis,* in which the seventh segment is over three times as long as the sixth ventrally. In one undescribed species of *Tenagogonus s. str.* from the Fiji Islands the posterolateral angle of the seventh segment is produced as a spinous process, a condition that occurs also in a species of *Eurygerris.*

Modifications of the other structures.

The size of body: As will be noted from table 8, the length of the body ranges from 19.5 mm. in *T. (L.) inermis* to 5.0 mm. in *T. (T.) pravipes bergrothi.* It has been observed that the reduction of the metasternum and pregenital segments are to a large extent responsible for the reduction in body size. In the larger species listed in the upper part of the table, the abdomen is more primitive and the metasternum is less reduced; in the smaller species listed in the lower part of the table, both the metasternum and the pregenital segments are more or less greatly reduced. It is interesting to note that there is a striking tendency among the larger species for the male to be larger than female and that this relation is reversed among the smaller species.

Table 8.—Length of body in species of *Tenagogonus.*

	Male	Female	Rostrum 3rd:4th
T. (L.) femoratus	19 mm. (wgd.)	17.6 mm. (wgd.)	5.0 :1
T. (L.) cursitans	19 mm. (wgd.)	16.4 mm. (wgd.)	5.0 :1
T. (L.) inermis	19.5 mm. (wgd.)	13.6 mm. (wgd.)	....
T. (L.) ciliatus	13–19.5 mm. (wgd.)	14.2 mm. (largest wgd.)	5.0 :1
T. (L.) lipovskyi	13.4 mm. (wgd.)	10.9 mm. (wgd.)	4.75:1
T. (L.) insularis	11.8 mm. (wgd.)	9.8 mm.	....
T. (L.) palauanus	9.0 mm. (wl.)	11.0 mm. (wl.)	3.85:1
T. (L.) borneensis	10.0 mm. (wgd.)	9.8 mm. (wgd.)	4.37:1
T. (L.) anadyomene	9.8 mm. (wl.)	12.0 mm. (wl.)	4.11:1
T. (L.) octopunctatus	9.2 mm. (wl.)	11.3 mm. (wl.)	4.11:1
T. (L.) rossi	6.9 mm. (wgd.)	7.6 mm. (wgd.)	3.91:1
T. (L.) minutus	8.6 mm. (wgd.)	....	....
T. (T.) kuiterti	8.7 mm. (wl.)	8.0 mm. (wl.)	3.70:1
T. (T.) zambezinus	8.5 mm. (wl.)	9.9 mm. (wl.)	....
T. (T.) divergens	7.6 mm. (wl.)	....	4.27:1
T. (T.) robustus	7.6 mm. (wl.)	7.4 mm. (wl.)	3.88:1
T. (T.) madagascariensis	7.3 mm. (wl.)	8.3–8.9 mm. (wl.)	4.00:1
T. (T.) albovittatus	6.7–7.4 mm. (wl.)	7.3–7.6 mm. (wl.)	3.50:1
T. (T.) kampaspe	5.3 mm. (wl.)	6.3 mm. (wl.)	3.17:1
T. (T.) pravipes bergrothi	5.0 mm. (wl.)	6.6 mm. (wl.)	3.84:1
T. (T.) fijiensis	5.3 mm. (wl.)	6.7 mm. (wl.)	3.17:1

wgd.=winged, wl.=wingless.

Rostrum: As noted from table 8, the length of the third segment in relation to the fourth segment has apparently decreased with reduction in size of the body accompanied by specialization of structures.

Subgenus *Tenagometra* Poisson

(Figures 407-415.)

Tenagometra Poisson, Mem. Inst. Sci. Madagascar A, 1(2):95 (1949) (as subgenus of *Tenagogonus*).

Type species: *Tenagogonus lanugineus* Poisson, monobasic.

Structures in wingless forms: Body relatively small. *Male much smaller than female.* Antenna without conspicuous sexual difference in length of first segment in relation to second. Pronotum not at all or feebly prolonged. *Mesonotum wholly exposed, posterior margin broadly rounded, lateral longitudinal margin defining mesonotum from mesopleuron distinct. Front leg with femur strongly arched and with a dark stripe on inner margin in male; tibia curved in male;* tarsus with first segment a little shorter than second. Abdomen relatively short, without connexival spine in both sexes. Abdominal spiracles on second to seventh placed closer to anterior margin than to posterior margin of each segment.

Male: Seventh segment with ventral apical margin broadly concave. Eighth segment with ventral apical margin feebly sinuate, broadly rounded on dorsal apical margin. Ninth segment with suranal plate simply narrowed near apex; pygophore rounded on apical margin; parameres vestigial. Endosoma with definitive dorsal plate thick, bifurcate apically, strongly thickened at base; ventral lobe short and lobate; lateral plates long and simple; basal segment of endosoma with a pair of two black processes near ventral apical margin on each side. (Description of the genitalia is based on an unidentified species of this subgenus.)

Female: Eighth segment ventrally largely covered by seventh ventrite, which is longer than the preceding segment. (The female genitalia were not examined.)

Distribution: Africa (Madagascar, East Africa).

The subgenus *Tenagometra* is distinguishable from the *Limnometra-Tenagogonus s. str.* complex by the following features:

(1) The antennae are short and without sexual differences in the proportional lengths of the first and second segments.

(2) The front leg is sexually dimorphic.

(3) The pronotum is not or feebly prolonged in the wingless forms.

(4) The mandibular and maxillary plates are almost completely fused.

(5) The lateral longitudinal suture between the mesonotum and mesopleuron is recognizable.

That this subgenus has probably arisen from *Tenagogonus s. str.* or a similar form is indicated by the fact that the lengths of the middle and hind leg segments resemble those of typical *Tenagogonus s. str.* species. The secondary reduction of the pronotum in wingless forms occurs also in *Tenagogonus (Tenagogonus) madagascariensis* independently of this subgenus, suggesting a similar evolutionary potentiality in this respect in the two subgenera.

It was found that in the *Limnometra-Tenagogonus s. str.* complex the males are larger than the females in the larger and more primitive species, and with reduction in body size and specialization of structures this relation has apparently been reversed so that in a great majority of species of *Tenagogonus s. str.* the female is larger than the male. In *Tenagometra,* the male is much smaller than the female as in *Tenagogonus s. str.*

While the division into *Tenagogonus s. str.* and *Limnometra* is quite artificial and purely for the taxonomic convenience, *Tenagometra* is a distinct natural group.

Genus *Tenagometrella* Poisson

(Figures 1, 416-420)

Tenagometrella Poisson, Rev. Zool. Bot. Afr., 56(1-2):171 (1957) (as subgenus of *Tenagogonus*).

Tenagometrella Hungerford and Matsuda, Univ. Kansas Sci. Bull., 39(9): 374 (1958) (as genus).

Tenagogonus Poisson, Bull. Mus. nat. Belg., 56(40):11-13 (1940) (in part).

Type species: *Tenagogonus grandiusculus* Poisson, by present designation.

Species examined: *T. grandiusculus* (Poisson), *T. longicornis* (Poisson).

Color pattern: Similar to that of *Tenagogonus,* but different in having a pale yellow median longitudinal stripe instead of black stripe on pronotum, and in the presence of two white oblong spots on mesopleural region.

Structures in wingless forms: Antennae and legs very long in male. Head including eyes a little wider than long. Eye with inner margin strongly emarginated. Antenna in male: very long; first segment longest, almost as long as total length of body; shorter than second and third segments together; second segment a little shorter than first; third segment a little shorter than second, ciliate on margins; fourth segment shortest, almost one third as long as third segment.* Antenna in female: a little longer than length of body; first segment longest, third segment longer than fourth segment but shorter than second. Antenniferous tubercles slightly dilated in front of eyes. Clypeus with basal margin distinct. Mandibular and maxillary plates distinguishable from each other. Rostrum slender and long, reaching middle of mesosternum; first segment about half as long as head; third segment over five times as long as last segment.

Pronotum prolonged to near posterior margin of mesonotum, relatively slender, broadly rounded on apical margin. Intersegmental suture between mesonotum and metanotum obliterated laterally. Mesosternum over three and a half times as long as metasternum; paired longitudinal sutures absent; median longitudinal sulcus distinct in anterior half of mesosternum. Metathoracic spiracle located at some distance from pronotum. Metanotum with lateral longitudinal elevation conspicuous, reaching dorsal end of metacetabular suture; median longitudinal sulcus distinct. Metasternum much longer than second ventral abdominal segment; omphalium highly reduced, located at apical third of metasternum; omphalial groove absent. Front leg slender; a little longer than body in male; femur and tibia slender, the latter slightly swollen apically, with a bare shallow depression near apex on inner margin; first and second tarsal segments subequal in length to each other, claws arising from apical fourth of second segment. *Middle leg in male with femur longer than total length of body,* about as long as tibia; tibia much over four times as long as first tarsal segment; first tarsal segment four times as long as second, claws slender, arising from near apex; middle leg in female much shorter than in male, but proportional lengths of leg segments are much like those in male. Hind leg with femur longer than middle femur in both sexes, a little over twice as long as tibia in male, less than twice as long as tibia in female; tibia about six times as long as first tarasl segment in female, about eight times as long as first tarsal segment in male; first tarsal segment a little over twice as long as second in both sexes.

Abdomen shorter than thorax, gradually narrowed posteriorly. First tergite with usual flattened W-shaped anterior margin; second to sixth segments subequal in length both dorsally and ventrally

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* This may possibly be due to a partial loss of the fourth segment from the specimen examined.

in both sexes, with a slender connexival spine in both sexes. Third to fifth abdominal spiracles placed at middle of each abdominal segment; ventral longitudinal margin of connexivum indistinct, represented by faint depressions; ventral median longitudinal carina absent.

Male: Seventh segment simply broadly concave on both dorsal and ventral apical margins. Eighth segment ventrally slightly exposed, broadly concave on ventral apical margin. Ninth segment with suranal plate simple; pygophore simply rounded on apical margin; parameres absent. Endosoma with definitive dorsal plate narrow, reaching apical margin, forked into two thick branches apically (the part of apical plate); ventral plate membranous, bilobed apically; lateral plates slender.

Female: Seventh segment longer than sixth ventrally, ventral apical margin feebly bisinuate. Eighth segment slightly exposed ventrally (genitalia were not examined).

Winged forms: Pronotum with humeri located far behind middle. Hemelytra with Sc connected with R + M at the point of separation into R and M.

Distribution: Africa (Belgian Congo, Liberia, Cameroons).

The genus *Tenagometrella* is distinguishable from the *Limnometra-Tenagogonus* complex by the following characteristics:

(1) The conspicuous sexual difference in lengths of the antennae and legs.

(2) A higher degree of reduction and different location of the omphalium.

(3) The yellow instead of black median longitudinal pronotal stripe.

The presence of sexual differences in the proportional lengths of the first and second antennal segments, the proportional lengths of leg and rostral segments, and the degree of specialization of the abdomen are much like those in the more specialized species of *Limnometra* or the more primitive species of *Tenagogonus s. str.* As already noted, there is no significant sexual difference in the proportional lengths of most antennal and leg segments although their absolute lengths are quite different. This fact suggests that the sexual difference lies primarily in the initial growth index b for those segments in allometry equation term. This genus has probably arisen from the *Limnometra-Tenagogonus* complex with acquisition of the above mentioned peculiar features.

Although Poisson (1957) included three species within the subgenus *Tenagometrella*, obviously *T. zambezinus* belongs to *Tenagogonus* (Hungerford and Matsuda, 1958). The specimens identified by Poisson as *T. grandiusculus* and *T. longicornis* at the University of Kansas very likely represent the female and male of the same species; they are provisionally treated as the same species in this study.

Tribe CYLINDROSTETHINI Matsuda

Color pattern: Black in ground color in majority of species, with longitudinal silvery stripe laterally on the thorax in most species.

Structures in wingless forms: Head between eyes widened posteriorly. Clypeal region well produced anteriorly, with basal margin lost, apical margin straight, connected with labrum by membranous region, thus apical margin appears to be separated from above labrum. Antenna much shorter than body, first segment about as long as or a little shorter than three following segments together; second segment longer than or subequal to third segment, third segment with a distinct basal peduncle; fourth segment curved beyond middle. Antenniferous tubercles divergent anteriorly. Eye with inner margin indented except in *Platygerris*. Mandibular and maxillary plates either indistinct from each other or completely fused. Rostrum short and thick, never extends beyond prosternum, third segment one and half to two and a half times as long as last segment.

Pronotum not prolonged, rather strongly widened posteriorly. Mesosternum without median longitudinal sulcus, anterior margin more or less produced at middle; paired longitudinal sutures recognizable anteriorly in some species of *Cylindrostethus* and *Potamobates*. Intersegmental suture between mesonotum and metanotum faint, forming a small subtriangular space anterior to metacetabular suture. Metanotum with median longitudinal sulcus distinct; lateral longitudinal suture nearly reaching metacetabular suture; metacetabular suture joined with dorsal posterior margin of mesonotum. Metasternum with distinct omphalium and omphalial groove leading onto metacetabular region except for *Platygerris*, in which the groove is absent. Front leg with femur thick basally; tibia arched in apical third, inner apical angle with inconspicuous process; tarsus with first segment greatly reduced. Middle leg with femur considerably longer than tibia; tarsus usually flattened and curved, first segment two and a half to seven times as long as second segment. Hind leg always shorter than middle leg; femur one and one fifth to three times as long as tibia; tarsus with first segment about as long as to nearly three times as long as second segment. *Claws of middle and hind legs present only in Cylindrostethus from the Eastern Hemisphere.*

Abdomen varies greatly in length. Anterior margin of first tergite flattened W-shaped. Well-developed connexival spines present only in *Cylindrostethus;* ventral margin (suture) of connexivum obscure or absent.

Male: Seventh segment with ventral apical margin emarginated at middle on concave apical margin; ventral surface either modified or unmodified. Eighth segment not greatly prolonged, or greatly prolonged and its ventral apical margin asymmetrical in some species. Ninth segment with suranal plate more or less greatly, asymmetrically modified on lateral margins; pygophore rotated in

TABLE 9.—Table of significant generic characters in Cylindrostethini.

	Cylindrostethus	Potamobates	Platygerris
27.......	(±)×	(±)×	(—)
29.......	(—)	(+)	(+)
39A......	(+)	(±)	(—)
42.......	(+)	(+)	(—)
45A......	(+)	(±)	(—)
46.......	(+)	(—)*	(—)
59.......	(+)	(—)	(—)
61B......	(±)×	(—)	(—)
61D......	(+)	(±)	(—)
62A......	(+)	(—)	(—)
62B......	(+)	(—)	(—)
64A, 65...	(+)	(—)	(—)
66B......	(±)	(—)	(—)
69A......	(±)	(—)	(—)
72A......	(+)	(—)	(—)
92.......	(+)	(—)	(—)
108, 116...	(±)×	(—)	(—)
125.......	0.25–0.55 :1	0.29–0.38 :1	0.35–0.42 :1
126.......	0.56–0.79 :1	0.63–0.72 :1	0.37–0.41 :1
127.......	3.1–6.8 :1	3.2–4.0 :1	2.5–3.4 :1
128.......	0.41–0.79 :1	0.49–0.69 :1	0.28–0.33 :1
129.......	1.0–2.0 :1	1.3–2.3 :1	1.8–2.9 :1
Total...	(+) 11 (±) 5 (—) 1	(+) 2 (±) 4 (—) 11	(+) 1 (—) 16 ....

* In *Potamobates thomasi* Hungerford the spiracles are placed closer to the anterior margin than to the posterior margin.

For the explanations of symbols see introduction and table 5.

some species, simply rounded on apical margin; parameres inconspicuous or greatly reduced. Endosoma elongate, with excessive apical prolongation in *Platygerris;* dorsal plate extending along dorsal margin of endosoma, bifurcate apically, ventral plate long, number of lateral plates inconstant, often absent.

Female: Seventh segment with ventral apical margin bisinuate, or excessively developed. First valvula well sclerotized, divided into basal thicker and apical narrow regions by median membranous area; inner lobe membranous or thinly sclerotized, long and narrow apically. Second valvula with lateral margin strongly sclerotized, apical half narrow, also strongly sclerotized, convergent apically beyond apical margin of intervalvular membrane, where it is also heavily sclerotized and broadly rounded or nearly straight. Vulva inconspicuous, membranous and narrow.

Winged forms: Pronotum long, humeri located at apical one third of pronotum. Hemelytra with Sc connected either with R + M at the point of separation into R and M, or with R + M basal to the point of separation of R and M.

Distribution: Central and South America, Oriental and Ethiopian regions.

Relationships of genera

As noted from the table of significant characters and from the discussion on evolution of the abdomen, antennae, and the rostrum, many characters exhibit linear evolutionary trends. Although the species of *Cylindrostethus* from the Western Hemisphere have taken a slightly different course of evolution in certain minor ways from the members of the same genus from the Eastern Hemisphere, *Potamobates* is apparently nothing but a more specialized group of *Cylindrostethus* from the Western Hemisphere. *P. thomasi* is apparently the border line species between the two genera, as is indicated by the location of the abdominal spiracles and the relatively long body, etc. As already seen, the leg and antennal segments in this species also quite deviate from the allomorphic lines for these segment of *Potamobates.* The genus *Platygerris* is more distinct with a greater and discontinuous reduction of the hind tibia in relation to the total length of the body, which is realized from quite different growth mechanisms for the leg segments as we have already seen. A strong dorsoventral flattening accompanied by broadening of the body emphasizes the distinctness of this genus from the other two. The relationships of the genera can be diagrammed as follows (diagram 4):

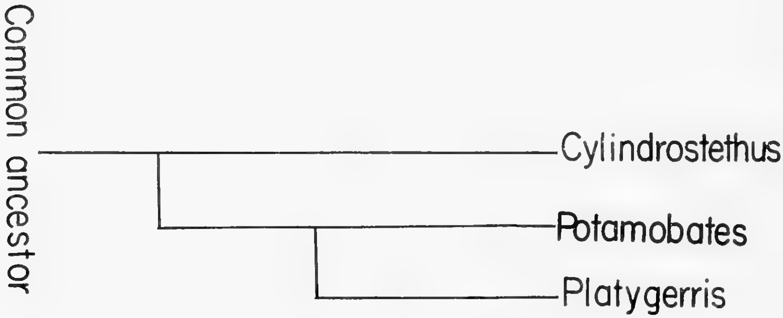

DIAGRAM 4.—Diagram showing the relationships of genera of the *Cylindrostethini.*

Evolutionary tendencies and characteristics peculiar to Cylindrostethini

(1) Because of the relatively short rostrum, which never extends beyond the prosternum, the median longitudinal groove for the reception of the rostrum has never arisen on the metasternum, and the anterior margin of the mesosternum has even become produced anteriorly at the middle in *Cylindrostethus.*

(2) The omphalium and the lateral groove of the omphalium leading onto the metacetabula persist in *Cylindrostethus* and *Potamobates,* although the groove is lost in the most specialized genus, *Platygerris.*

(3) The ventral apical margin of the seventh segment of the female is excessively developed in the more specialized genera.

(4) An asymmetrical modification of the suranal plate of the male has occurred in varying degrees in most species of all genera.

(5) The ventral apical margin of the eighth segment of the male has become asymmetrically modified in the more specialized genera.

(6) The claws have become lost in all species occurring in the Western Hemisphere.

In addition to the above mentioned peculiar evolutionary tendencies, the following structural characteristics common to all genera serve to distinguish this tribe from the other three tribes:

(1) The pronotum in wingless forms is never prolonged.

(2) The first tarsal segment of the front leg is greatly reduced,

due to a smaller growth ratio for the first segment than for the second segment.

(3) The fourth antennal segment is short and curved beyond the middle.

(4) The apical margin of the clypeus is loosely connected with the base of the labrum by a membranous region.

(5) The hemelytra arise from near apical third of the pronotum; thus the humeri are located considerably more caudad than in the other tribes.

(6) The intersegmental suture between the mesonotum and metanotum in wingless forms is obscure but traceable laterally, forming a subtriangular space anterior to the metacetabular suture, which is well impressed and fused with the dorsal posterior margin of the mesonotum.

Modifications of the abdomen in Cylindrostethini

(Figs. 433-446, 447-451, 470-480, 483, 495-500)

Since the species of *Cylindrostethus* from the Western Hemisphere are different from those of the same genus from the Eastern Hemisphere in certain respects, the evolution of the abdomen is discussed separately for each group. In the three genera of Cylindrostethini occurring in the Western Hemisphere the modification of the genital segments is rather beautifully traceable.

(A) Modifications of the abdomen of Cylindrostethini from the Western Hemisphere.

The male seventh segment: In *Cylindrostethus* the seventh segment is at least as long as, or usually longer than the preceding segment ventrally on the median longitudinal axis. In *Potamobates* the length of the seventh segment in relation to the sixth is smallest in *thomasi* and the relative length becomes 2.5 to 3 times as long as the preceding segment in six out of nine species; the relative length of the seventh to the sixth is as 2.5 to 3.5:1 in three species of *Platygerris.* The connexival spine is well developed in *Cylindrostethus* although it is rather inconspicuous in some species; in *Potamobates* and *Platygerris* it has been greatly reduced or lost. The ventral apical margin is simple and concave. An emargination at the middle of the ventral apical margin is small in some species of *Cylindrostethus;* in *Potamobates* the median emargination is least conspicuous in *thomasi;* it becomes progressively more conspicuous in other species of the genus with more specialized abdominal structures (figs. 475-480); the median emargination is conspicuous in all species of *Platygerris.*

The male eighth abdominal segment: In *Cylindrostethus* the ventral apical margin is simple and concave or feebly produced medially, and the segment is not prolonged. The segment in *Potamobates* has become prolonged, its ventral basal region is depressed and the ventral apical margin is modified; first a small rather inconspicuous process occurs on the left side of the ventral apical margin (*unidentata, horváthi,* figs. 476, 478), then with further prolongation of the eighth segment the process arises near the middle and the right posterior angle became greatly modified (*williamsi, variabilis,* figs. 479, 480). Simultaneously with the modification on the apical margin, the basal depression on the ventral surface became more well marked. In *asymmetricus* (fig. 483) and *depressus* of *platygerris* the segment is not greatly prolonged and has a conspicuous process on the right side of the ventral apical margin, as in some species of *Potamobates;* in *caeruleus* of the same genus (*Platygerris*) the eighth segment is enormously prolonged (fig. 496), although the ventral apical margin is relatively simple.

The male ninth segment: The suranal plate in *Cylindrostethus* is symmetrical; the process on each lateral margin of the suranal plate is more and more directed cephalad in the more specialized species of the genus (figs. 436-440). In *Potamobates* the ninth tergite has become rotated for about 45 degrees and the processes are asymmetrical and more conspicuous on the left side, although they are inconspicuous in *thomasi* and *unidentatus* (figs. 475-480); with further development of the process on the left side of the ninth tergite, its apex comes to contact the asymmetrically modified apical margin of the eighth segment in some species of *Potamobates* (figs. 479, 480). The ninth segment is not rotated in *Cylindrostethus,* the rotation becomes apparent in *Potamobates unidentatus* and the degree of rotation becomes greater in other species of *Potamobates* except for *thomasi,* in which the segment is only feebly rotated; in *Platygerris* the ninth segment is rotated in all species.

The female seventh segment: The ventral apical margin of the seventh segment in the female of *Cylindrostethus* is simple, feebly produced at the middle; the connexival spine is also retained in all species. In *Potamobates* the connexival spine is retained, but the ventral apical margin is highly modified and the eighth segment is completely hidden by the excessive development of the ventral apical margin except for *horváthi* and *thomasi.* In *Platygerris* the connexival spine becomes even less conspicuous, asymmetrical or lost on the left side, and the excessive development of the ventral apical margin covers the ventral surface of the eighth segment.

(B) Modifications of the abdomen in *Cylindrostethus* from the Eastern Hemisphere.

The male seventh segment (figs. 435, 441-446): The ventral apical margin of the seventh segment is simple and concave, without a median emargination, in all species. The degree of specialization is thus best seen in relative length of the seventh to the sixth segment. In *productus* and *costalis* the seventh segment is considerably shorter than the sixth on the median longitudinal axis, followed by *persephone* (7th:6th::7:9), *naiades* (8.5:10), *vittipes* (7.5:7.5), and *sumatranus* (9:7.5); the connexival spine is very long in *costalis* and *productus,* still conspicuous in *naiades,* but in all other species it has become increasingly inconspicuous. In *sumatranus* and *persephone* the seventh segment is considerably longer than the sixth segment dorsally.

The male eighth segment: The ventral apical margin of the eighth segment is greatly produced posteriorly; the dorsal apical margin is rounded, feebly notched in *naiades* and *persephone.*

The male ninth segment: The suranal plate has basal lateral process which are asymmetrical, the process on the left side is always larger. There is no conspicuous difference in degree of modification among the species, but in *costalis, productus* and *vittipes* the modification is more conspicuous than in other three species.

The female seventh segment (figs. 447, 451): The degree of specialization, as indicated by the relative lengths of the seventh and sixth segments, is in the following order from more primitive to more specialized: *productus, costalis, vittipes, naiades, persephone,* and *sumatranus.* In *productus* the seventh segment is much shorter than the sixth, in the next three species the seventh segment is a little longer than the sixth, and in the last two species the seventh segment is much longer than the sixth. The connexival spine is long in *productus, naiades* and *persephone,* inconspicuous in *vittipes* and *sumatranus.* In *sumatranus* the connexivum is folded back on the dorsum.

Modifications of the other structures in Cylindrosethini.

The rostrum: In the species of *Cylindrostethus* from the both Hemispheres the third segment is over twice as long as the last segment in the relatively large species with more primitive abdomens, a little less than twice as long as the last segment in the smaller species with more specialized abdomens except for *sumatranus;* in *Potamobates* the third segment is about twice as long as in the great majority of species; in *Platygerris* the third segment is less than one and a half times as long as the last segment in all species. There is thus, throughout the tribe, a clear tendency toward the reduction of the length of the third segment in relation to the fourth, correlated with specialization of the abdomen and with reduction in size of the body.

The antennae: In *Cylindrostethus* the second segment is definitely longer than the third in all species. In *Potamobates* the second segment is about as long as the third in all species except for *thomasi,* in which the second segment is distinctly longer than the third as in *Cylindrostethus.* In *Platygerris* the second segment is definitely shorter than the third in all species. The length of the second segment in relation to the third thus appear to have become smaller in the course of evolution.

Genus *Cylindrostethus* Fieber

(Figs. 17-18, 115-116, 127, 134, 154, 421-459)

Cylindrostethus Fieber, Europ. Hemip., p. 33 (1861) (no species mentioned).
Cylindrostethus Mayr, Verh. Zool. Bot. Ges. Wien, 15:444(1865) (one species described).
Cylindrostethus Kirkaldy, Entomologist, 30:258(1897).
Cylindrostethus Bergroth, Ent. Month. Mag., 18:258(1902).
Cylindrostethus Kirkaldy and Torre-Bueno, Proc. Ent. Soc. Washington, 10:210(1908).
Cylindrostethus Schmidt, Stett. Ent. Zeit., 76:361(1915).
Cylindrostethus Torre-Bueno Spolia Zeylandica, 13:226(1925).
Cylindrostethus Drake and Harris, Ann. Carnegie Mus., 23:179-240(1934).
Cylindrostethus Lundblad, Arch. Hydrobiol. Suppl. 12, Tropische Biennengewässer, 4, pp. 392-394(1933).
Cylindrostethus Kuitert, Univ. Kansas Sci. Bull., 28(1):135-138(1942).
Cylindrostethus Drake, Amer. Mus. Nov. 1579:2-3(1952).
Cylindrostethus Hungerford, Proc. 10th Intern. Congr. Ent., pp. 344, 346(1958).
Hydrobates Erichson, in Schomburgk, Faun. Brit. Guiana, 3:614(1848) (generic name preoccupied, type species, *Hydrobates linearis* Erichson).
Janias Distant, Ann. Mag. Nat. Hist., 8(5):145(1910) (type species, *Janias elegantulus* Distant).

Type species: *Cylindrostethus fieberi* Mayr, first included species.

Species examined: *C. bassleri* Drake, *C. bilobatus* Kuitert, *C. costalis* Schmidt, *C. erythropus* (Herrich-Schaeffer), *C. hungerfordi* Drake and Harris, *C. linearis* (Erichson), *C. naiades* Kirkaldy, *C.*

nietneri Schmidt, *C. palmaris* Drake and Harris, *C. persephone* Kirkaldy, *C. productus* Spinola, *C. regulus* (B.-White), *C. sumatranus* Lundblad, *C. vittipes* Stål.

Color pattern: Ground color somewhat variable, a reddish brown, pale brown and nearly black. Pronotum with a yellow patch or median yellow longitudinal stripe. Mesopleuron with either longitudinal band of silvery pubescence or without it. Mesonotum with more or less distinct paired longitudinal stripes in some species.

Structures in wingless forms: Body elongate and cylindrical. Head between eyes strongly narrowed between anterior half of eyes, then widened posteriorly. Eye large, exserted, emarginated on inner margin. Antenna robust and relatively short; first segment longer than two following segments together; second segment longer than third; fourth segment much longer than third, cylindrical, curved beyond middle. Antenniferous tubercles divergent anteriorly. Clypeus with basal margin completely lost. Mandibular and maxillary plates obscurely defined from each other. Rostrum reaching posterior margin of head; third segment one and a half to two and a half times as long as last segment.

Pronotum hexagonal in shape, shorter than head, posterior margin nearly straight, posterolateral margin oblique. Mesonotum long, posterior margin broadly rounded and feebly notched at middle, with a faint median longitudinal sulcus. Mesosternum twice to three and a half times as long as metasternum, simply convex, simple and concave on posterior margin; paired longitudinal sutures distinct anteriorly in some species, anterior margin roundly elevated and more or less strongly produced forward at middle in some species. Metanotum with median longitudinal sulcus distinct, lateral elevation reaching almost well marked metacetabular suture. Metasternum a little longer than second ventral abdominal segment; omphalium reduced but the groove leading onto metacetabula always well marked near posterior margin; lateral opening of the groove covered with hairs in most species. Front leg with femur thick, a little longer than tibia except for *vittipes* in which they are subequal in length; tibia in apical third slightly thickened apically, apical margin with a notch, with inconspicuous process at inner apical angle; tarsus with second segment two to four times as long as first segment, claws arising from near apex. Middle leg longer than hind leg; femur about as long as to much shorter than length of body, one and a quarter to twice as long as tibia; tibia a little less than twice to about three times as long as first tarsal segment; tarsus flattened, first tarsal segment three to seven times as long as second segment; second segment with a pair of long hairs on dorsal margin near apex. Hind leg with femur about one and one fifth to a little over twice as long as tibia; tibia five to over ten times as long as tarsus; first tarsal segment as long as to twice as long as second tarsal segment. Inconspicuous claws from near apex of middle and hind tarsi occur in species from Eastern Hemisphere.

Abdomen long, nearly parallel sided. First tergite with W-shaped anterior margin, much shorter than second tergite, second to sixth tergites subequal in length to each other. Connexivum more or less reflexed. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment. Ventral longitudinal suture of connexivum represented by rather obscure longitudinal impression on each segment; median longitudinal carina distinct.

Male: Seventh segment with more or less conspicuous connexival spine, ventral apical margin concave or with a small median emargination on concave posterior margin. Eighth segment with dorsal apical margin nearly straight or gently rounded except for *naiades* and *sumatranus,* in which it is notched at middle; ventral apical margin simple and concave, slightly produced at middle. Ninth segment not rotated; suranal plate narrowed apically; processes at base asymmetrical, with acute apex directed either cephalad or caudad; pygophore simply rounded on apical margin; parameres rather weakly developed but distinct. Endosoma with definitive dorsol plate extending along the entire dorsal margin of endosoma only *(productus),* extends from apical margin to basal margin, bifurcate at base and connected with membranous ventral plate which is coiled within endosoma *(linearis, erythropus, palmaris, naiades);* lateral plates short, located as basal angles of endosoma. (Description of the male genitalia is based on *producutus, linearis, erythropus, palmaris, naiades*).

Female: Seventh segment with connexival spine as in male, ventrally about as long as or longer than sixth segment, ventral apical margin more or less bisinuate, more or less produced posteriorly at middle. Eighth segment well exposed both dorsally and ventrally; first valvula with inner lobe membranous, acutely pointed, haired on inner margin in *erythropus;* outer lobe well sclerotized except for median small membranous area, haired throughout inner margin and apical half of outer margin in *erythropus,* apex simply narrowed, ramus attached on outer margin of process from ninth tergite. Second valvula well sclerotized, rounded apically; intervalvular membrane with apical margin well sclerotized and broadly rounded, continuous with outer margin of second valvulae; ramus arising from the middle of inner margin of each valvula, rather short. (Description of the female genitalia is based on *productus* and *erythropus*).

Winged forms: Pronotum widest at apical one third. Hemelytra with vein Sc connected with R + M at the point of branching into R and M.

Distribution: South America (Brazil, British Guiana, Bolivia, Peru), West Indies (Trinidad), and the Oriental region (Burma, Cambodia, Celebes, Ceylon, Philippines, Sumatra), and the Ethiopian region (Liberia).

The species of *Cylindrostethus* from the Western Hemisphere are different from the members of the same genus from the Eastern Hemisphere in the following points:

(1) The species of *Cylindrostethus* from the Eastern Hemisphere have the basal processes of the suranal plate acute and always directed caudad, while they are directed cephalad in the species from the Western Hemisphere.

(2) The middle and hind femora in *Cylindrostethus* from the Eastern Hemisphere are as long as the body except for *productus* and *costalis,* while they are distinctly shorter than the length of body in all species from the Western Hemisphere.

(3) The hind leg is much longer than the body in the species from the Eastern Hemisphere, while it is about as long as length of body in the species from the Western Hemisphere.

(4) A conspicuous modification of the anterior margin of the mesosternum is much more pronounced in some species of *Cylindrostethus* from the Western Hemisphere than in the species from the Eastern Hemisphere.

(5) The claws are absent in the middle and hind legs in the species from the Western Hemisphere.

The differences in lengths of leg and antennal segments between the two groups of *Cylindrostethus* is mainly due to the differences in initial growth indices for these segments, as have already been observed.

Genus *Potamobates* Champion

(Figs. 19, 117, 135, 155, 460-480, 490-493)

Potamobates Champion, Biol. Centr. Amer., Rhynch., 2:154(1901)
Potamobates Esaki, Ann. Mus. Nat. Hung., 23:251-257(1926)
Potamobates Hungerford, Bull. Brooklyn Ent. Soc., 27(5):228(1932)
Potamobates Drake and Harris, Ann. Carnegie Mus., 23:223-229(1934)
Potamobates Kuikert, Univ. Kansas Sci. Bull., 28(1):139-142(1942)
Potamobates Drake, Proc. Biol. Soc. Washington, 67:227-230(1954)

Type species: *Potamobates unidentatus* Champion, by subsequent designation (Drake and Harris 1934, in the above bibliography).

Species examined: *P. bidentatus* Champion, *P. horváthi* Esaki, *P. thomasi* Hungerford, *P. peruvianus* Hungerford, *P. tridentatus* Esaki, *P. unidentatus* Champion, *P. variabilis* Hungerford, *P. williamsi* Hungerford *P. woytkowskyi* Hungerford.

Color Pattern: Body above predominantly black, mottled with pale yellow markings or stripes. Head black along inner margins of eyes and clypeal region in most species. Pronotum with a median longitudinal yellow stripe or patch, which is confined to anterior lobe in winged forms. Front leg pale yellow, with black stripe at least on inner margin. Mesonotum with or without a median longitudinal yellow stripe and a pair of yellow markings on either side of middle, lateral limit of black area clothed with silvery pubescence. Abdomen above largely dark fuscous to black, each tergite with median yellow spot in some species. Body beneath pale yellow.

Structures in wingless forms: Head wider across eyes than long, strongly narrowed at middle between eyes. Eye exserted posteriorly, large, inner margin emarginated posteriorly, covering anterolateral angle of pronotum. Antenna short; first segment definitely longer than two following segments together; second segment subequal to third one except for *thomasi,* apex truncate; fourth segment fusiform, slightly bent at middle or apically. Antenniferous tubercles bent forward, short. Mandibular and maxillary plates completely fused. Rostrum short, scarcely extending beyond prosternum, third segment about twice as long as fourth segment.

Pronotum with posterior margin nearly straight or feebly sinuate, strongly widened anteriorly. Mesonotum with posterior margin roundly produced. Mesosternum three and one third to a little over four times as long as metasternum; paired longitudinal sutures faint but traceable. Metanotum with median longitudinal sulcus distinct at least anteriorly. Metasternum with omphalium vestigial, lateral groove extends onto metacetabulum where it opens, the opening either covered by a tuft of hairs or without them. Front leg with femur thick basally, then gradually thinned apically; tibia incurved and slightly thickened apically, apical margin notched, inner apical angle produced, with apical longitudinal depression on both outer and inner surfaces; tarsus slightly curved; first segment highly reduced; second segment three to three and a half times as long as first segment; claws arise from near apex. Middle leg longer than hind leg; femur about as long as or a little shorter than body, a little less than one and a half times as long as tibia; tibia three times to a little less than twice as long as first tarsal segment; first tarsal segment four times to a little over three times as long as second tarsal segment; apical half of tibia and tarsus flattened and curved, shallowly sulcate on inner margin; second tarsal segment without claws, with a pair of long hairs arising from upper margin near apex. Hind leg with femur about as long as middle femur, twice as long as to a little less than one and a half times as long as tibia; tibia several times as long as tarsus; tibia and tarsus simply narrowed apically; first tarsal segment one and one third to nearly two and one half times as long as second tarsal segment; second tarsal segment with a pair of long hairs arising from upper margin near apex; claws absent.

Abdomen relatively short, subparallel sided or a little narrowed posteriorly. First tergite with W-shaped anterior margin, about as long as or longer than second tergite, second to fifth tergites subequal in length, short, sixth tergite a little longer than fifth tergite. *Ventrites with intersegmental suture obscure in some species.* Abdominal spiracles placed a little closer to posterior margin than to anterior margin in all species except for *thomasi,* in which spiracles placed much closer to anterior margin than to posterior margin of each segment. Ventral connexival suture obscure.

Male: Seventh segment much longer than sixth segment, both dorsally and ventrally except for *thomasi;* connexival spine absent or present as short obtuse projection; ventral apical margin always with double emarginations. Eighth segment cylindrically produced posteriorly, almost as long as all preceding segments together in some species, posterior margin more or less greatly modified except for *thomasi,* ventral surface depressed basally in some species, ventral apical margin always with denticular projection, right posterior angle produced in bizzare shape. Ninth segment rotated to right in all species except for *thomasi,* in which it is only slightly rotated; suranal plate asymmetrically modified on sides (conspicuous process on left side); parameres vestigial. Endosoma long; dorsal plate thick but not bifurcate apically, bifurcate at upper basal angle where it is articulated with sclerotized basal plate; ventral plate sclerotized at least basally; lateral plates simple, sclerotized at middle of dorsal region of endosoma above dorsal plate. (Description of the genitalia is based on *horváthi, unidentatus, thomasi*).

Female: Seventh segment with ventral basal margin acutely produced cephalad at middle, with more or less well developed connexival spine, ventral surface excessively developed, assuming various shapes on apical margin, covering completely eighth segment above in most species (in *thomasi* apical margin with a pair of long processes and eighth segment well exposed ventrally); first valvula with inner lobe membranous, folded beneath outer lobe basally, apical half simply narrowed apically; outer lobe robust, basal half of which distinct by oblique narrow membranous region from distal part where is simply narrowed and narowly rounded apically; ramus arising from distal end of basal sclerotized part of outer lobe, connected with process of ninth segment on its outer margin. Second valvula with lateral area in its basal half well sclerotized and continuous with apical margin of intervalvular membrane, where is well sclerotized and freely produced posteriorly in the middle, apical half of second valvula narrow, directed mesad, apex rounded; ramus long. (Description of the female genitalia is based on *thomasi* and *peruvianus*.)

Winged forms: Pronotum widest at apical one third, then broadly rounded apically. Hemelytra with Sc united with R + M before the point of branching into R and M respectively.

Distribution: Central and South America (British Honduras, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Peru, Venezuela).

The genus *Potamobates* is more primitive than related genus *Platygerris* in:

(1) Retention of the lateral groove of the omphalium leading onto the metacetabula.

(2) The less flattened body.

The genus *Potamobates* is more specialized than *Cylindrostethus* in:

(1) The fusion of the mandibular and maxillary plates.

(2) The less uniform pregenital segments.

(3) Higher degree of modification of the genital segments in both sexes.

(4) The location of the abdominal spiracles, *i. e.*, they are at or a little behind the middles of the segments in a great majority of species.

(5) The loss or great reduction of the connexival spine.

(6) The rotation of the male genital segments.

Genus *Platygerris* Buchanan-White

(Figs. 20, 118, 136, 156, 481-489, 494-504)

Platygerris Buchanan-White, Ent. Month. Mag., 20:36(1883)
Platygerris Hungerford, Bull. Brooklyn Ent. Soc., 28(4):178-182(1932) (Key to species).

Type species: *Platygerris depressus* Buchanan-White, monobasic.

Species examined: *P. asymmetricus* Hungerford, *P. depressus* B.-White, *P. caeruleus* Champion.

Color pattern: Predominantly black. Head with an orange yellow spot on vertical region. Pronotum with a yellowish median longitudinal stripe, which is confined to anterior lobe in winged forms. Mesothorax with lateral longitudinal stripe composed of silvery pubescence. The color pattern similar to *Potamobates,* but with more dark areas in this genus.

Structures in wingless forms: Body short and strongly flattened. Head between eyes strongly widened posteriorly. Eye indented posteriorly. Antenna short and thick; first segment about as long as three following segments together; second segment linear, thickened anteriorly, apex truncate; third segment always shortest; fourth segment always curved near apex. Antenniferous tubercles thick, divergent anteriorly. Clypeus with basal margin completely lost, anterior margin straight. Mandibular and maxillary plates completely fused. Rostrum short and thick; third segment one and a half times as long as last segment.

Pronotum about as long as head in middle, much wider than head across eyes, posterolateral margin broadly rounded; *propleura widely separated from each other leaving broad prosternum between.* Mesonotum long, wider than pronotum. Mesosternum seven to nine times as long as metasternum; paired longitudinal sutures absent. Metanotum short, median longitudinal sulcus absent; lateral longitudinal elevation weakly developed, not reaching metacetabular suture. Metasternum short; omphalium vestigial but distinct, lateral groove of omphalium absent. Front leg with femur strongly thickened at base, somewhat dorsoventrally depressed in male of *caeruleus,* with a small tubercle at middle on inner margin of *depressus;* tibia always incurved apically, with rather inconspicuous process at inner apical angle, rather strongly longitudinally impressed on inner margin at apex; first tarsal segment short, second segment at least twice as long as first, claws arising from near apex. Middle leg a little longer than hind leg; femur much longer than body, about two and a half times as long as tibia; tibia flattened at least in apical half, strongly thickened apically, about one and a half times as long as first tarsal segment; tarsus strongly flattened, first segment about three times as long as second; claws absent. Hind leg with femur a little longer than middle femur, a little over three times as long as tibia; tibia at least twice as long as tarsus which is flat, first tarsal segment about twice to nearly three times as long as second segment. Claws absent.

Abdomen slightly narrowed apically in both sexes. First and second tergites have their anterior margins produced anteriorly; third to seventh tergites progressively longer posteriorly; second to sixth ventrites a little longer in female than in male; connexival spine lost. Abdominal spiracles, as well as ventral suture of connexivum, were not studied (the lateral regions of the abdomen are flanked by the metacetabular region and basal leg segments).

Male: Seventh segment ventrally strongly depressed, ventral apical margin concave and excavate at middle. Eighth segment has spinous process to the left of middle of apical margin in *asymmetricus* and *depressus;* very long and cylindrical, and without process on apical margin in *caeruleus.* Ninth segment always rotated to the right; suranal plate has process like projection on left side and the process meets apically with the apex of process of eighth segment; pygophore rounded apically; parameres vestigial in *P. asymmetricus.* Endosoma with proximal membranous area not well developed (*asymmetricus*) or developed (*caeruleus*); definitive dorsal plate extending along dorsal margin of endosoma, articulated with ventral plate at basal dorsal margin of endosoma; ventral plate sclerotized, long and paired, reaching apex of endosoma; lateral plates located in apical region of endosoma; dorsal margin of endosoma sclerotized at middle above dorsal plate.

Female: Seventh segment long ventrally, ventral basal margin acutely produced, trilobed apically and folded on ventral side of eighth segment, with a rather conspicuous spinous process on right side beneath connexivum and with coarse bristles on each side of dorsal posterior margin in *asymmetricus* and *caeruleus;* with small process on both sides near lateral lobes of ventrites, of which the one on right side a little more conspicuous in *depressus.* First valvula with inner lobe thinly sclerotized, with narrow apex directed mesad; outer lobe robust and well sclerotized, divided into basal and apical halves by intervening membranous area, of which apical area acutely pointed; ramus arises from distal end of basal sclerotized area, connected with process of ninth tergite on its outer margin, apical end of the latter acutely produced on inner edge. Second valvula also divided into basal and distal strongly sclerotized areas by a narrow intervening membranous area, apical half narrow and curved, apex rounded; intervalvular membrane with apical margin straight, strongly sclerotized, the sclerotization extends lateroanteriorly and continuous with basal half of second valvula; ramus arising along inner margin of basal sclerotized area, extending cephalad and again caudad along the ramus of eighth segment, reaching about middle of the process of ninth tergite. Vulva membranous and narrow. (Description of the female genitalia is based on *P. asymmetricus.*)

Structures in winged forms: Pronotum widest at the apical one third. Vein Sc connected with R + M before the point of branching into R and M respectively.

Distribution: Central America (Costa Rica, Mexico)

This genus is the most specialized in the Cylindrostethini and can readily be distinguished from the other two genera by the absence of the omphalial groove and the flattened body. The extraordinarily long middle and hind femora appear to be produced by extraordinarily high growth ratios for these segments.

Tribe CHARMATOMETRINI Matsuda

Color pattern: Predominantly reddish brown in most species, with a black longitudinal stripe on pronotum in some species.

Structures in wingless forms: Head between eyes widened posteriorly. Clypeus with basal margin always lost, directly connected with labrum anteriorly. Antennae shorter than length of body, first segment about as long as or shorter than two following segments together except for *Charmatometra,* in which it is distinctly longer than two following segments together, second segment always shortest, third segment with a distinct basal peduncle, always longer either than second or fourth. Antenniferous tubercles rather small, rounded on outer margins. Mandibular and maxillary plates at least partially distinct from each other. Rostrum extending beyond prosternum; third segment three to four times as long as fourth segment.

Pronotum always fully prolonged, posterior margin rounded. Mesosternum with median longitudinal sulcus absent; paired longitudinal suture lost in most species. Intersegmental suture between mesonotum and metanotum often obscure laterally. Metanotum with median longitudinal sulcus distinct; lateral longitudinal elevation absent; metacetabular suture poorly developed, not extending dorsally. Metasternum with omphalium and omphalial groove leading onto metacetabula always present. Front leg with femur simple; tibia sometimes with a conspicuous inner apical process (*Charmatometra*); tarsus with first segment half as long as to about as long as second segment; claws arising preapically. Middle leg longer than hind leg; femur shorter than tibia in all species except for *Charmatometra* and *Eobates.* Tarsus with first segment three to a little over five times as long as second segment. Hind leg with femur a little less than twice as long as tibia; tarsus with first segment a little longer than to over two and a half times as long as second segment.

Abdomen moderately long. First tergite always with nearly straight anterior margin enclosing first abdominal spiracle in anterolateral corner of first tergite. Seventh segment without connexival spines; ventral margin of connexivum obscure.

Male: Seventh segment with ventral apical margin subquadrangularly incised, without median emargination, at least a little longer than sixth segment ventrally. Eighth segment more or less prolonged in most species, concave on ventral apical margin, without conspicuous modification on ventral surface. Ninth segment with suranal plate simple; pygophore with apical margin rounded; parameres simply arched and well developed, present in all species. Endosoma with dorsal plate extending along dorsal margin of endosoma, either fused or not fused with basal plate which supports more or less membranous ventral lobe; lateral plates sometimes large.

Female: Seventh segment with ventral apical margin more or less concave in most species, produced medially in some more specialized species of *Brachymetra.* Eighth segment with first valvula with narrow and short membranous inner lobe folded beneath outer lobe; apex of outer lobe simply rounded. Second valvula apically directed mesad, rounded at apex, extending beyond round apical margin of intervalvular membrane. Vulva with broader basal region and apical narrow projection. *Vestigial third valvula is recognizable.*

Winged forms: Pronotum with humeri located at a little behind middle. Hemelytra with well formed embolium. Sc connected with R + M at the point of separation into R and M.

Distribution: Central and South America.

Table 10.—Table of significant generic characters in Charmatometrini.

	Charmatometra	Eobates	Brachymetra
17.......	(+)	(+)	(—)
27.......	(+)	(—)	(—)
33.......	(+)	(—)	(±)
46.......	(+)	(—)	(—)
123.......	(O)	(O)	(×)
125.......	1:1	0.56–0.66 :1	0.54–0.69 :1
126.......	0.82–0.84 :1	0.92:1	1.03–1.12 :1
127......	4.0–5.1 :1	3.1–3.2 :1	3.1–4.7 :1
128......	0.56–0.59 :1	0.61–0.66 :1	0.45–0.60 :1
129......	2.0–2.2 :1	1.2–1.3 :1	1.4–2.9 :1
Total...	(+) 4 (—) 0 (O) 1	(+) 1 (—) 3 (O) 1	(+) 0 (±) 1 (—) 3 (×) 1

For the explanations of symbols see introduction and table 5.

Relationships of genera

The three genera are closely related. *Charmatometra* is more primitive than the other two in at least three characters, as noted from the table of significant characters. *Brachymetra* has apparently orginated from a *Charmatometra*-like ancestor with the loss of the characters 17 and 27 in the table, and the shift in location of the abdominal spiracles which has been accompanied by the reduction of the pregenital abdominal segments. The genus *Brachymetra* can reasonably be regarded as a specialized group of *Charmatometra.* The genus *Eobates,* however, is a more distinct genus having a peculiar color pattern and different relative length of the hind tarsal segments from the other two genera. As have already been observed the different proportional lengths of the hind tarsal segments (and possibly also the middle tarsal segments) in *Eobates* has resulted from significantly different growth patterns for these segments from the equivalents of the other two genera. The relationships of the genera thus can be diagrammatically shown as follows (diagram 5):

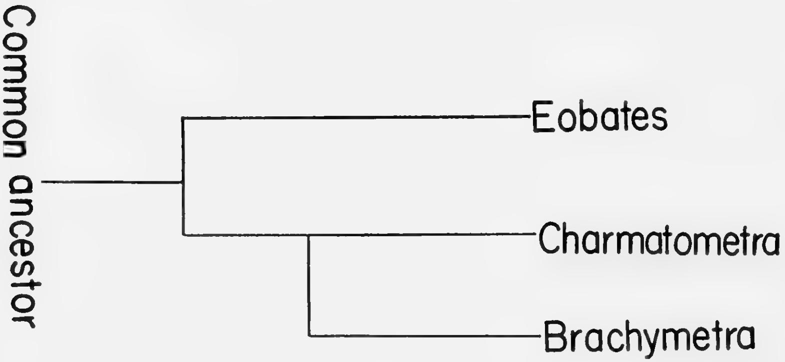

Diagram 5.—Diagram showing the relationships of genera of the Charmatometrini.

Characters peculiar to Charmatometrini

(1) The pronotum in wingless forms is prolonged and secondary reduction has never occurred.

(2) The metasternum has the omphalium as well as the omphalial groove in all species of all genera.

(3) The connexival spine is absent and presumably has never arisen.

(4) In the middle leg the growth ratio for the femur is apparently greater than that for the tibia. Inheriting this growth potential the tibia has become relatively longer (longer than the femur in absolute lengths) with reduction in body size in phylogeny.

In addition to the above-mentioned peculiarities the straight anterior margin of the first abdominal tergite, etc., distinguish this tribe from the other tribes of Gerrinae.

Modifications of the abdomen in Charmatometrini

The male seventh segment: The degree of specialization of the segment is indicated by the length of the seventh segment relative to the sixth. In *B. kleopatra, B. shawi,* and one unidentified species of *Brachymetra* from Brazil the length of the seventh in relation to the sixth ranges 7.5:6.5 or 4.5:5.5 to 5:8 ventrally, and 7:7 to 5:6.5 dorsally. In smaller species it ranges from 5.5:3.5 in *anduzei* to 9:4.5 in *albinerva incisa* ventrally, or 7:4 in *lata* to 11.5:5 in *anduzei* dorsally. In *Charmatometra* and *Eobates* the ventral apical margin is simple and concave as in more primitive species of *Brachymetra*, and the relative lengths of the seventh and sixth segments are 15:11 and 10.5:7.5 ventrally respectively.

The male eighth segment: In *Brachymetra* the ventral apical margin is concave and the segment is shorter than the seventh in *kleopatra* and *shawi*, while it is about as long as the seventh in *lata*, *albinerva incisa*, and in an unidentified species from Brazil. The highest degree of prolongation of the eighth segment is found in *unca* and *anduzei*, in which the segment is longer than the seventh and the ventral apical margin is roundly produced posteriorly. In *Charmatometra* and *Eobates* the eighth segment is, as in more primitive species of *Brachymetra*, shorter than the seventh ventrally.

The female seventh segment: In such larger species of *Brachymetra*, as *kleopatra* and *shawi*, the seventh segment is less than one and five sevenths times as long as the sixth segment ventrally and the ventral apical margin is concave; dorsally the seventh segment is as long as the sixth in *shawi;* in smaller and more specialized species the proportional lengths of the seventh and sixth segments range from 10:6.3 in *lata* to 15:6 in *unca* ventrally, 5.7:5 in one unidentified species from Brazil to 11:5.5 in *anduzei* dorsally. The ventral apical margin is more or less produced posteriorly at the middle to cover the eighth segment above, ending in an acute median tip in *unca*. In *Charmatometra*, the seventh ventrite is one and four elevenths times as long as the sixth ventrite, *i. e.*, the seventh ventrite is relatively a little shorter than in the more primitive and larger species of *Brachymetra*. In *Eobates* the seventh is one and two third times as long as sixth segment; dorsally the seventh segment is just a little longer than the sixth (8:7) and the ventral apical margin is concave.

The female eighth segment: The eighth segment with the valvifers together are concave on the apical margin in the larger species of *Brachymetra*, such as *shawi*, *kleopatra*, and a species from Brazil; in *anduzei* they are together produced posteriorly and elevated, and the surface is clothed with long hairs (fig. 538). In *Charmatometra* the apical margin of the valvifers is produced. In *Eobates* it is produced.

Genus *Charmatometra* Kirkaldy

(Figs. 21, 113-114, 127, 133, 152, 505-516)

Charmatometra Kirkaldy, Ann. Soc. Ent. Belg., 48:509(1899).
Charmatometra Drake and Harris, Ark. Zool., 28B(2):3(1935).
Charmatometra Drake and Harris, Iowa Sta. Jour. Sci., 15(3):237-240(1941)
Charmatometra Hungerford, Ent. News, 64(7):172-175(redescription).
Brachymetra Kirkaldy, Entomologist, 31(420):101-102(1898)(described *B. bakeri*).

Type species: *Brachymetra bakeri* Kirkaldy, by original designation.

Species examined: *Charmatometra bakeri* (Kirkaldy).

Color pattern: Predominantly reddish brown, silvery pubescent on propleuron, mesopleuron and lateral part of abdominal tergites.

Structures in wingless forms: Head between eyes strongly narrowed medially. Eye superposed on pronotum posteriorly. Antenna with first segment thickened anteriorly and truncate at apex, a little shorter than three following segments together; second segment simply thickened anteriorly; third segment a little over one and a half times as long as second; fourth segment elongate fusiform, a little shorter than third. Antenniferous tubercles small, rounded on lateral margins. Clypeus strongly bent forward, basal margin completely lost. Mandibular plate distinct from maxillary plate partially. Maxillary plate large, its anterior margin broadly rounded. Rostrum relatively short, third segment a little over three times as long as last one.

Pronotum with anterior lobe widened anteriorly; posterior lobe narrowed apically, apical margin broadly rounded. Intersegmental suture between mesonotum and metanotum distinct laterally. Mesosternum about five times as long as metasternum; paired longitudinal sutures distinct, divergent posteriorly; median longitudinal sulcus absent. Metanotum short, median longitudinal sulcus distinct. Metasternum a little less than twice as long as second ventrite; omphalium small, but with distinct lateral groove leading onto metacetabulum and its lateral opening covered by a tuft of straight hairs. Front leg with femur slightly narrowed apically, with a small laevigate tubercle near apex on inner margin; tibia strongly widened apically, longitudinally depressed on inner apical area, apex outwardly divided into two parts by deep longitudinal cleft, of which inner part rather conspicuously produced; tarsus long, first and second segments subequal in length; second one with small claws arising subapically. Middle leg with femur longer than length of body, distinctly longer than tibia; tibia somewhat curved and flattened apically, about three times as long as first tarsal segment; tarsus somewhat flattened, first segment four to about five times as long as second segment, with distinct apical claws. Hind leg with femur about as long as middle femur, a little less than twice as long as tibia; tibia about six times as long as first tarsal segment, with a row of short hairs on inner margin; tarsus about one fourth as long as tibia; first tarsal segment over twice as long as second segment.

Abdomen oblong ovate. First tergite considerably longer than second tergite; second to seventh tergites progressively longer posteriorly, but quite uniform in shape. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment; ventral longitudinal suture of connexivum obliterated; median ventral longitudinal carina absent.

Male: Seventh and eighth segment well exposed both dorsally and ventrally, broadly concave on seventh ventral posterior margin. Ninth segment with suranal simple; pygophore rounded on apical margin; parameres well developed but simple in shape. Endosoma with dorsal plate apically fused with large, round apical plate, basally giving support to ventral plate, which is small and membranous except on lateral sclerotized areas; lateral plates robust, extending along ventral margin of endosoma and apically narrowed. (Description of the genitalia is based on *C. bakeri.*)

Female: Seventh segment longer than sixth segment. Eighth segment well exposed both dorsally and ventrally. First valvula with inner lobe small and short, folded beneath basal region of outer lobe; outer lobe not divided into basal and apical sclerotized parts, apex rounded; ramus arising from near apex of outer lobe, extending along outer margin of process of ninth tergite. Second valvula with apex rounded, extending beyond first valvula and apical margin of intervalvular membrane where it is rounded and thinly sclerotized, ramus relatively short. *Reduced third valvula arises from crescent shaped sclerite above the process of ninth tergite, and it is sclerotized apically.* Vulva with broader basal region and median elongate apical region extending beyond middle of first valvula.

Winged forms: Pronotum wide, humeri located at a little behind middle, broadly rounded on apical margin. Intersegmental suture between mesonotum and metanotum distinct between metathoracic spiracle and wing base. Hemelytra were not available for study.

Distribution: South America (Colombia, Ecuador, Venezuela.)

Genus *Brachymetra* Mayr

(Figs. 23, 113-114, 133, 152, 527-547)

Brachymetra Mayr, Verh. Zool. Bot. Ges. Wien, 15:445(1865).
Brachymetra Shaw, Univ. Kansas Sci. Bull., 21:221(1933).
Brachymetra Harris and Drake, Proc. Ent. Soc. Washington, 47(7):211-212 (1945).

Type species: *Halobates albinervis* Amyot and Serville, by original designation.

Species examined: *B. anduzei* Drake and Harris, *B. albinervis incisa* Shaw, *B. kleopatra* Kirkaldy, *B. lata* Shaw, *B. shawi* Hungerford and Matsuda, *B. unca* Shaw, one unidentified species from Brazil.

Color pattern: Predominantly reddish brown. Head without black marking. Pronotum occasionally with a median longitudinal black stripe and black lateral margin (*anduzei*).

Structures in wingless forms: Head narrowed between eyes. Eye exserted posteriorly, inner margin feebly concave, posterior half of inner margin covering anterolateral angle of pronotum. Antenna with first segment always longest; second segment always shorter than third segment; third segment more slender than second segment; fourth segment shorter than third segment. Antenniferous tubercles small. Clypeus with basal margin lost. Mandibular and maxillary plates distinct from each other and of about same sizes. Rostrum rather short, third segment about three to four times as long as last segment.

Pronotum with apical margin broadly rounded. Intersegmental suture between mesonotum and metanotum often obliterated. Mesosternum four and two thirds to six times as long as metasternum; paired longitudinal sutures absent; median ventral longitudinal sulcus absent or indistinct. Metanotum with short and indistinct median longitudinal sulcus. Metasternum distinctly longer than second ventrite; omphalium reduced, lateral groove leading onto metacetabula distinct and the lateral opening covered with a tuft of hairs. Front leg rather long; femur simply narrowed apically; tibia slightly swollen apically, bipartite by an oblique longitudinal cleft in apical region, inner apical process inconspicuous; first tarsal segment a little shorter or about half as long as second segment; claws arising from apical third of second segment and with arolium. Middle leg with femur always shorter than tibia, also always shorter than hind femur; tibia three and a half to seven times as long as first tarsal segment; first tarsal segment four and five sevenths to three and one fifth times as long as second segment. Hind leg with femur a little less than twice as long as tibia; tibia seven and a half to four times as long as first tarsal segment; first tarsal segment over two and a half times to one and a half times as long as second segment.

Abdomen ovate, gradually narrowed apically. First tergite much longer than second tergite and with a more or less prominent tubercle at middle of posterior margin in females of some species; second tergite with anterior margin slightly produced; third to sixth tergites more or less uniform in shape and length; second to sixth ventrites more or less uniform in shape and length. Abdominal spiracles placed at middle of each segment; ventral margin (longitudinal suture) of connexivum absent.

Male. Seventh and eighth segments well exposed both dorsally and ventrally, posterior margin subquadrangularly concave in both segments. Ninth segment with suranal plate simply narrowed apically; pygophore rounded on apical margin; parameres well developed, simply arched. Endosoma with definitive dorsal plate bifurcate at base (basal plate) and on apical margin of endosoma; ventral plate membranous apically, relatively short; lateral plates simple, large in some species. (Description of the male genitalia is based on *kleopatra, lata* and *shawi.*)

Female: Seventh segment longer than sixth segment both dorsally and ventrally. Eighth segment well exposed both dorsally and ventrally in most species. First valvula without well differentiated inner lobe, apex acute, ramus arising from near apex; crescent shaped sclerite loosely connected with apex of the process from ninth tergite and with apical region of ramus of second valvula. Second valvula with apical margin rounded, extending beyond apical margin of intervalvular membrane where it is thinly sclerotized and rounded; ramus arising from beyond middle of second valvula. Vulva with broader basal area and provided with a median narrow production. (Description of the female genitalia is based on *lata.*)

Winged forms: Pronotum elongate subpentagonal in shape, widest at middle in most species. Intersegmental suture between mesonotum and metanotum is often confluent with elevated lateral margin of metanotum which reaches base of wing.

Distribution: South America (Bolivia, Brazil, British Guiana, Ecuador, Panama, Paraguay, Peru, Venezuela) and Trinidad.

This genus differs from *Charmatometra* in the following characteristics:

(1) The intersegmental suture between the mesonotum and metanotum is usually unrecognizable laterally in wingless forms.

(2) The middle tibia is longer than the middle femur.

(3) The body size is smaller.

Genus *Eobates* Drake and Harris

(Figs. 22, 113-114, 133, 152, 517-526)

Eobates Drake and Harris, Proc. Biol. Soc. Washington, 47:175-176(1934) (described *E. morrisoni* which is a synonym of *Brachymetra vittatus* Shaw, 1933).

Brachymetra Shaw, Univ. Kansas Sci. Bull., 21:224(1933) (described *B. vittatus* which belongs to *Eobates*).

Type species: *Eobates morrisoni* Drake and Harris, by original designation.

Species examined: *E. vittatus* (Shaw).

Color pattern: Pale yellow in ground color. Head with a median and paired black lateral longitudinal stripes. Pronotum with paired black longitudinal stripes and lateral margin black. Connexivum along lateral margin black. Tergites black except for posterior margins paler. Mesothorax with lateral black longitudinal stripe; metanotum black.

Structures in wingless forms: Head between eyes narrowed. Eye with inner margin feebly sinuate. Antenna with first segment longer than two following segments together; second segment slightly thickened apically; third segment a little longer than second one; fourth segment shorter than third. Antenniferous tubercles small. Clypeus with basal margin lost. Mandibular and maxillary plates distinct from each other, the latter larger than the former and broadly rounded on anterior margin. Rostrum relatively long, distinctly extending beyond posterior margin of prosternum; third segment about four times as long as last segment.

Pronotum slightly widened at apical third, posterior margin broadly rounded. Intersegmental suture between mesonotum and metanotum barely recognizable laterally. Mesosternum about four and a half times as long as metasternum; without either median longitudinal sulcus or paired longitudinal sutures. Metanotum with median longitudinal sulcus distinct. Metasternum distinctly longer than second ventrite; omphalium highly reduced but lateral groove well marked at apical third of metasternum, lateral opening of the groove clothed with a tuft of straight hairs. Front leg with femur narrowed apically; tibia with apex slightly swollen, with an oblique sulcus near apex, inner apical angle slightly produced; first tarsal segment about two thirds as long as second segment, second segment with claws arising from apical one fourth of the segment. Middle leg with femur a little longer than tibia or than body; tibia about four times as long as first tarsal segment; first tarsal segment about three times as long as second, both segments strongly curved, second segment with apical claws. Hind leg with femur over one and a half times as long as tibia; tibia about four and a half times as long as tarsus, or over eight times as long as first tarsal segment; first tarsal segment a little longer than second segment.

Abdomen ovate. First tergite long, posterior margin concave; second to sixth tergites subequal in length at middle. Abdominal spiracles placed at middle of each segment; ventral median longitudinal elevation absent.

Male: Seventh tergite much longer than sixth tergite; seventh ventrite broadly subrectangularly concave on apical margin. Eighth segment well exposed both dorsally and ventrally, broadly concave on ventral apical margin. Ninth segment with suranal plate rounded on apical margin, largely hidden beneath eighth tergite; pygophore rounded on apical margin; parameres visible on either side of pygophore. (The genitalia were not examined.)

Female: Seventh tergite a little longer than sixth tergite; seventh ventrite much longer than sixth ventrite, concave on apical margin. Eighth segment exposed both dorsally and ventrally. (The genitalia were not examined.)

Winged forms: Pronotum with humeri located at a little behind middle, posterolateral margin feebly concave. Intersegmental suture between mesonotum and metanotum running along distinctly ridged lateral margin of metanotum as far as wing base.

Distribution: Central and South America (Haiti, Peru).

The genus *Eobates* is distinct from the other genera of Charmatometrini by the following characteristics:

(1) The quite distinct color pattern.

(2) The first tarsal segment of the hind leg is only slightly longer than the second segment.

Tribe EOTRECHINI Matsuda

Color pattern: Reddish brown to black in ground color in most species. Pronotum and mesonotum usually provided with a yellow longitudinal stripe or stripes.

Structures in wingless forms: Head between eyes not conspicuously widened posteriorly. Clypeal region strongly bent ventrad in *Amemboa,* basal margin distinct except for *Amemboa.* Antennae slender, first segment as long as or longer than second, usually considerably longer than second, third and second subequal in length in most species, fourth segment longer than third in most species. Antenniferous tubercles reduced in *Amemboa.* Mandibular and maxillary plates distinct from each other except for *Amemboa.* Rostrum extending beyond prosternum, third segment at least twice as long as third.

Pronotum not prolonged. Mesosternum with median longitudinal sulcus distinct or obscure; paired longitudinal sutures lost in more specialized genera. Intersegmental suture between mesonotum and metanotum laterally obliterated in *Amemboa.* Metanotum with median longitudinal sulcus distinct; metacetabular suture dorsally not reaching intersegmental suture between mesonotum and metanotum; lateral longitudinal suture not reaching intersegmental suture. Metasternum varies greatly in degree of reduction in length; omphalium present but always without lateral omphalial groove leading onto metacetabula. Front leg with femur and tibia greatly modified in males of *Amemboa* and *Chimarrhometra.* Middle leg with femur about one to one and a half times as long as tibia; first tarsal segment about twice to half as long as second segment; *claws arise apically, or from near apex, or from near middle of second segment.* Hind leg longer than middle leg, or about as long as middle leg, or shorter than middle leg; tibia strongly reduced in more specialized genera (less than half as long as femur); first tarsal segment twice to half as long as second segment; *claws arise from various positions on second segment as in middle leg.*

Abdomen with anterior margin of first tergite always represented by flattened W-shaped suture. Connexival spine of seventh segment always absent; ventral margin of connexivum obscure or lost.

Male: Seventh segment without median emargination on ventral apical margin, greatly prolonged in more specialized genera. Eighth segment greatly prolonged in more specialized genera. Ninth segment with suranal plate greatly modified in *Amemboa;* pygophore modified on apical margin in *Amemboa* and *Chimarrhometra;* parameres present except for *Amemboa.* Endosoma with round and relatively large apical plate loosely connected with dorsal plate; ventral plate, when present, totally membranous.

Female: Seventh segment prolonged both dorsally and ventrally in more specialized genera. Eighth segment with first valvula long, well differentiated into inner and outer lobes; the former reaching about the middle of the latter. Second valvula extending beyond apical margin of intervalvular membrane. Vulva largely membranous, narrow in *Onychotrechus,* rather broad in *Amemboa.*

Winged forms: Pronotum relatively short and humeri located near middle in *Amemboa*, elongate and humeri located behind middle of pronotum in *Eotrechus* and *Onychotrechus.* Sc_2 is joined to R beyond the point of branching of basal R + M in more specialized genus *Amemboa.*

Distribution: The oriental region. The discontinuous extension of the Malayan fauna into Peninsular India and Ceylon, and a marked difference between the fauna of Ceylon and Southern India on the one hand and that of Northern India on the other are well known. Pradhan (1952) has already discussed the distribution of the genus *Amemboa* in relation to this problem. *Onychotrechus* and *Eotrechus* exhibit the same distributional pattern as *Amemboa,* which occurs in Southern India, Burma, China, Thailand, Annam, Sumatra, Java, Mindanao, Luzon and Formosa. *Chimarrhometra* and *Rheumatotrechus*, however, are known from the Himalayas.

Relationship of genera

Eotrechus is obviously the most primitive genus as seen from table 11, and the ancestral species of this tribe was probably much like *Eotrechus,* as is evident from the overwhelmingly large numbers of primitive characters in this genus. From this *Eotrechus*-like ancestor the other four genera have become distinct with acquisition of new characters through reduction and modification of the preexisted ones. *Onychotrechus* has apparently become a distinct group with acquisition of peculiar shape and position of the claws, etc., although this genus has still retained a relatively large number of primitive characters. In *Amemboa* the specialization of structures has reached its maximum, for only one primitive character is retained out of twenty-five tabulated. *Chimarrhometra* is also highly specialized although it retains more primitive characters than *Amemboa. Rheumatotrechus,* which I failed to examine, may possibly be a close relative of *Chimarrhometra.* All the genera of this tribe are not in a linear phylogenetic relationship, and no one genus can be directly derived from any other. They are possibly remnants of a once diverse group. The phylogenetic relationships of genera can be roughly expressed by diagram 6.

Evolutionary tendencies more or less peculiar to the Eotrechini

(1) The pronotum is not prolonged in wingless forms. Presumably the prolongation has never arisen.

(2) The ventral apical margin of the seventh abdominal segment

TABLE 11.—Table of significant generic characters in Eotrechini.

	Eotrechus	Onychotrechus	Chimarrhometra	Amemboa
4......	(+)	(+)	(—)	(—)
9......	(+)	(+)	(+)	(—)
11......	(+)	(+)	(+)	(—)
16......	(+)	(—)	(—)	(—)
27......	(+)	(+)	(—)	(—)
30......	(+)	(+)	(—)	(+)
33......	(?)	(+)	(+)	(—)
39A.....	(+)	(±)	(±)	(—)
45A.....	(+)	(±)	(—)	(—)
45B.....	(+)	(—)	(+)	(—)
46......	(+)	(—)	(—)	(—?)
52......	(+)	(—)	(—)	(—)
58......	(+)	(—)	(—)	(—)
63A.....	(+)	(±)	(—)	(—)
67, 68A..	(+)	(+)	(+)	(—)
69A, B..	(+)	(+)	(—)	(—)
74......	(+)	(+)	(—)	(—)
76....	(+)	(—)	(—)	(—)
92....	(+)	(+)	(?)	(—)
97....	(+)	(+)	(—)	(—)
99....	(+)	(—)	(±)	(±)
101....	(+)	(+)	(—)	(—)
103B...	(+)	(+)	(+)	(—)
111A...	(+)	(—)	(±)	(±)
112....	(+)	(±)	(+)	(—)
125....	1:1	0.36-0.42 :1	0.63:1	0.54-0.75 :1
126....	0.97:1	0.66-0.68 :1	0.70:1	0.66-0.72 :1
127....	1:1*	0.33-0.44 :1	2.20:1	1.9-2.27 :1
128....	1.16:1	0.56-0.62 :1	0.56:1	0.39-0.44 :1
129....	1:1*	0.33-0.50 :1	1.33:1	1.36-1.57 :1
Total..	(+) 24 (—) 0 (?) 1	(+) 13 (±) 4 (—) 8	(+) 7 (±) 3 (—) 14 (?) 1	(+) 1 (±) 2 (—) 21 (—?) 1

* According to Esaki (1928).

For explanations of plates see introduction and table 5.

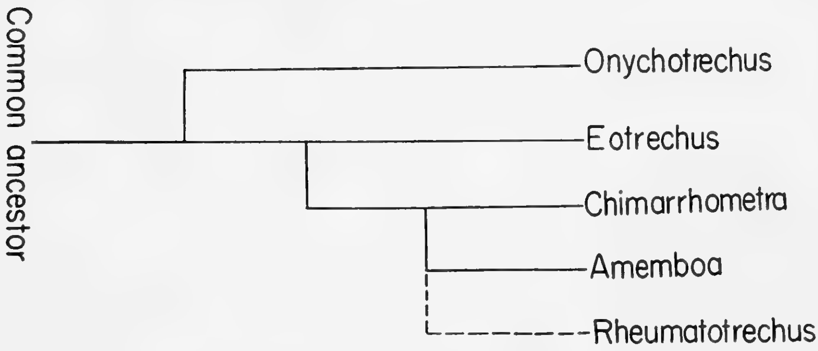

Diagram 6.—Diagram showing the relationships of genera of the Eotrechini.

of the male has never become doubly emarginated in the more specialized forms.

(3) The apical margin of the pygophore has become highly modified in the more specialized genera (*Chimarrhometra, Rheumatotrechus, Amemboa*).

(4) The hind coxa has become longer than wide in the specialized genera, *Onychotrechus, Amemboa.* This tendency is also noted in certain groups of Halobatinae and Ptilomerinae.

(5) The vein Sc_2 has become joined with R + M before the point of separation into R and M in the more specialized genus, *Amemboa,* due to more distal separation of the R + M vein into R and M veins. This tendency is observed also in Gerrini and Cylindrostethini.

In addition to the above-mentioned tendencies, the absence of the connexival spine, of the omphilial groove even in the most primitive genus *Eotrechus,* the large round apical plate of the endosoma, and the absence or poor development of the ventral plate in the apical segment of the endosoma separate this tribe from the other three tribes of the Gerrinae.

Modifications of the abdomen in Eotrechini

The most primitive pregenital segments are noted in *Eotrechus,* in which the segments are subequal in length to one another and the abdominal spiracles are placed closer to the anterior margin than to the posterior margin of each segment; in the other three genera the first to sixth segments have become increasingly shorter roughly in the order of *Onychotrechus, Chimarrhometra* and *Amemboa;* the abdominal spiracles have become located at the middle of each segment, and the total lengths of the abdomens in these genera are considerably shorter than in Eotrechus; in the males of *Amemboa* and *Onychotrechus* the ventral surface is longitudinally depressed at the middle.

The male seventh segment: In *Eotrechus* (fig. 548) the ventral apical margin is simply concave and a little shorter than the sixth ventrite on the median longitudinal axis. In *Onychotrechus* the seventh segment is about one and a half times as long as the sixth ventrally. In *Chimarrhometra* (figs. 572, 574) the seventh segment is about two and one fifth times as long as the sixth ventrally. In *Amemboa* (figs. 598, 603) the seventh segment is two and a half to four and a half times as long as sixth. In no species does there occur a small median emargination on the apical margin ventrally.

The male eighth segment: The eighth segment in *Eotrechus* is shorter than the seventh ventrally; in *Onychotrechus* the eighth segment is a little longer than the seventh ventrally; in *Amemboa* and *Chimarrhometra,* however, the eighth segment is greatly prolonged and cylindrical, telescoping the ninth segment at least basally.

The male ninth segment: The ninth segment in *Eotrechus* is provided with the styloide (figs. 551, 552). This structure has apparently been lost in all other genera of the Gerridae. The pygophore in *Eotrechus* and *Onychotrechus* is simply rounded on the apical margin. In *Amemboa* the apical margin has become more or less greatly modified. It is simply rounded only in one species from Thailand (unidentified, fig. 594), in which the pregenital and eighth segments are more primitive than in other species of the genus; in all other species the apical margin of the pygophore is always with a medially produced process and the ventral surface is elevated on the median longitudinal axis. The highest degree of modification is noted in another unidentified species from Thailand (fig. 593), in which the median process on the apical margin is most conspicuous and with a greatly modified rounded lobe on either side of the median process. In *Chimarrhometra* the modification of the apical margin of the pygophore is even more conspicuous than in *Amemboa* (figs. 572, 574, 576). The suranal plate is simple in *Eotrechus, Onychotrechus* and *Chimarrhometra;* in *Amemboa* the basal lateral margin has become greatly modified and conspicuous in *horváthi, lyra,* etc. (fig. 607), although it has remained much less modified in an unidentified species from Thailand (fig. 594). The parameres have been lost in *Amemboa* only; in *Chimarrhometra* it is greatly developed and modified (fig. 576). A possible functional substitution of the modified basal lateral region of the suranal plate for the parameres in *Amemboa* has already been discussed.

Female: Since the female specimens of *Eotrechus* and *Chimarrhometra* are not available for study, the comparison of the abdomens in this tribe cannot be complete. It can, however, be said that the seventh segment in *Onychotrechus* is less prolonged than in *Amemboa.* No conspicuous modification, besides the prolongation of the segment, has occurred in these two genera.

Modification of other structures in Eotrechini

As in most other genera of the Gerridae, the length of the third rostral segment relative to the fourth is greatest in the most primitive and the largest (in size) genus *Eotrechus* (4.1:1); in *Onychotrechus* the relative lengths range from 2.86:1 to 3.50:1, and the ratios are definitely greater than in *Amemboa* (2.1:1 to 2.54:1); in *Chimarrhometra* the relative lengths are 3.7:1. In the male of *Chimarrhometra* the front femur is greatly thickened, and in males of *Amemboa* the degrees in modification of the front leg vary from relatively slightly modified condition in an unidentified species from Thailand (fig. 578) to the most highly specialized condition in the femur and tibia of another unidentified species from Thailand (fig. 577). The degree of reduction of the metasternum is least in *Eotrechus* (mesosternum:metasternum :: 1.5:1), and is progressively more pronounced roughly in the order of *Chimarrhometra, Onychotrechus* and *Amemboa.*

Genus *Eotrechus* Kirkaldy

(Figs. 25, 127, 153, 548-558)

Eotrechus Kirkaldy, Entomologist, 35:137(1902).
Eotrechus Distant, Faun. Brit. Ind., Rhynch., 2:182(1904).
Eotrechus Bergroth, Jour. Bombay Nat. Hist. Soc., 24(1):179(1915).
Eotrechus Esaki, Ann. Mag. Nat. Hist., ser. 10(2):509(1928).

Type species: *Eotrechus kalidasa* Kirkaldy, by original designation.

Species examined: *E. kalidasa* Kirkaldy.

Color pattern: Head with a yellow crescent shaped spot. Pronotum with a pair of lateral and median yellow stripes only on anterior lobe. Mesonotum without silvery pubescence.

Structures in winged forms: Head including eyes a little wider than long, uppersurface widened between eyes. Antenna slender and long, all segments about equal in length. Antenniferous tubercles slightly rounded on lateral margin, apex not reaching base of clypeus. Clypeus with basal margin well defined. Mandibular and maxillary plates distinct from each other, mandibular plate extending above maxillary plate anteriorly; maxillary plate with anterior margin broadly rounded. Rostrum long and slender, third segment a little less than four times as long as last segment.

Pronotum in winged form obscurely divided into anterior and posterior lobes, humeri located at apical third of pronotum, broadly rounded on apical margin, strongly elevated posteriorly in posterior lobe. Prosternum relatively long. Hemelytra with vein Sc_2 united to R + M at the point of divergence into R and M respectively. Mesosternum about one and a half times as long as metasternum; paired longitudinal suture extends posteriorly as far as base of metasternal apophyses, median longitudinal sulcus well marked. Primary intersegmental suture between mesonotum and metanotum obliterated laterally. Metacetabular suture not well developed dorsally but well marked on either side of wing. Metasternum relatively long, concave on posterior margin; omphalium highly reduced but distinct, lateral groove of omphalium absent. Front leg with femur slender, slightly thinned apically; tibia much more slender than femur, apical region slightly thickened, without either process or constriction near apex; first and second tarsal segments subequal in length, claws arising apically, with conspicuous arolium. Middle leg with femur slender, about as long as tibia; first and second tarsal segments subequal in length (Esaki, 1928). Hind leg a little longer than middle leg; femur a little shorter than tibia; first and second tarsal segments about equal in length (Esaki, 1928).

Abdomen in male: Relatively long and highly generalized. Second ventrite about half as long as metasternum. Second to seventh segments ventrally subequal in length. Abdominal spiracle placed distinctly closer to anterior margin than to posterior margin of each segment from second to seventh segment. Ventral longitudinal suture (ventral margin) of connexivum obliterated in first two segments. Ventrites without median longitudinal impression.

Male: Seventh connexival segment without spine, ventral apical margin of seventh segment simply concave. Eighth ventrite shorter than seventh ventrite, concave on apical margin, eighth tergite broadly rounded on apical margin. Ninth segment with suranal plate narrow and simple; pygophore with conspicuous styloide on each side; parameres slender, apically rounded. Endosoma with definitive dorsal plate bifurcate at base, thickened on lower margin near base, apically reaching near apical margin of endosoma, not fused with large apical plate; lateral plates simple and long; without basal plate; ventral plate (?) membranous and short. (Description of the genitalia is based on *kalidasa*).

Female: Specimen was not available for study.

Distribution: Burma.

The genus *Eotrechus*, which is represented by only one species, *E. kalidasa*, has the following peculiar primitive characteristics:

(1) The prosternum is relatively long.

(2) All the antennal segments are subequal in length.

(3) The mesosternum is only one and a half times as long as the metasternum.

(4) The sternal and pleural regions of the mesothorax are distinctly defined by paired longitudinal sutures, which reach posteriorly to the bases of the mesosternal apophyses.

(5) The second to seventh ventrites are subequal in length.

(6) The hind leg is longer than the middle leg.

(7) The tibia is a little longer than the femur in the hind leg.

(8) The claws arise apically in all legs.

(9) The pygophore is provided with the styloide.

(10) The apical plate of the endosoma is separated from the dorsal plate.

The genus, however, is specialized in high degree of reduction of the omphalium and the loss of the lateral groove leading from the omphalium onto the metacetabular regions. This genus is apparently a relict.

Genus *Onychotrechus* Kirkaldy

(Figs. 26, 127, 153, 559-571, 599, 602)

Onychotrechus Kirkaldy, Entomologist, 36:44-45(1903).
Onychotrechus Distant, Faun. Brit. Ind., Rhynch., 2:182-183(1904).
Onychotrechus Esaki, Ann. Mag. Nat. Hist., Ser. 10(2):508(1928).
Gerris Kirkaldy, Entomologist, 34:117(1901) (described *Gerris* (*Limnometra*) *sakuntala*, which was assigned to *Onychotrechus* by Distant, 1904).

Type species: *Onychotrechus rhexenor* Kirkaldy, by original designation.

Species examined: *O. sakuntala* (Kirkaldy), *O. rhexenor* Kirkaldy.

Color pattern: Yellowish brown in ground color. Head above with a pair of black longitudinal stripes. Pronotum and propleuron each with two dark fuscous stripes, which are continuous onto mesonotum and mesopleuron. Mesopleuron with a longitudinal stripe of silvery pubescence between the dark stripes. Abdomen above predominantly dark fuscous.

Structures in wingless forms: Head between eyes much longer than wide, uppersurface convex, widened posteriorly. Eye with inner margin emarginate in posterior half. Antenna slender, first segment longer than second; second and third segments subequal in length; fourth segment a little longer than third. Antenniferous tubercles inconspicuous. Clypeus with basal margin distinct. Mandibular and maxillary plates clearly separated from each other, mandibular plate subtriangular, covering apically basal half of upper margin of maxillary plate. Rostrum with third segment over three times as long as last segment.

Pronotum about as wide as head including eyes, posterior margin broadly convex. Intersegmental suture between mesonotum and metanotum distinct both dorsally and laterally. Mesonotum with posterior margin feebly concave; median longitudinal sulcus recognizable posteriorly, but difficult to recognize due to presence of golden hairs. Mesosternum almost six times as long as metasternum, median longitudinal sulcus distinct only in anterior half. Paired longitudinal sutures distinct anteriorly, posterior margin of metasternum concave. Metacetabular suture poorly developed, not reaching lateral longitudinal suture of metanotum dorsally. Metanotum with median longitudinal sulcus indistinct, overgrown by golden hairs; lateral longitudinal elevation continuous with abdominal connexivum posteriorly, obliterated before posterolateral angle of mesonotum. Metasternum about twice as long as second abdominal ventrite; omphalium present at posterior one third of metasternum. Front leg slender; femur with a black protuberance at apical one fourth of inner margin in female of *rhexenor;* tibia slightly swollen at apex; second tarsal segment about twice as long as first segment, claws arising from apical one third of second segment, with a fine apically curled arolium. Middle leg about as long as hind leg; femur simply narrowed apically, about one and a half times as long as tibia; tibia about five to six times as long as tarsus; tarsus with first segment about half as long as second, claws well developed and with a simple long arolium, arising from apical one third of second segment. Hind leg slender, as slender as middle leg; femur over one and a half times as long as tibia; tibia about five times as long as tarsus; first tarsal segment about half as long as second segment, claws arising from apical one third of second segment, well developed and with a simple arolium. *Mesocoxa and metacoxa relatively long.*

Abdomen rather strongly narrowed posteriorly. Connexivum rather strongly reflexed. Abdominal segments not uniform in length and shape. First tergite much longer than second tergite; tergites increasingly longer in posterior segments, so are ventrites; fourth to seventh ventrites with median longitudinal depression in male. Abdominal spiracles placed at middle of each segment.

Male: Seventh ventrite with apical margin concave. Eighth segment well developed, oblique on dorsal margin, concave on apical margin. Ninth segment with suranal plate simple; pygophore well exposed ventrally; parameres short and robust. Endosoma with dorsal plate fused with paired round apical plates on apical margin of endosoma; lateral plates slender, ventral lobe totally membranous, without sclerotized basal support. (Description of the genitalia is based on *sakuntala.*)

Female: Seventh segment well developed both dorsally and ventrally, over three times as long as sixth segment ventrally in *sakuntala.* Eighth segment ventrally partly exposed; first valvula with inner lobe simply narrowed apically, short, about half as long as outer lobe, apex with a mass of long hairs; outer lobe simply narrowed apically, acute at tip; ramus on outer margin of outer lobe arising from about apical one fourth of the lobe, indistinguishably fused with process of ninth tergite. Second valvula with apex narrowly rounded, extending beyond apical margin of intervalvular membrane which is rounded; intervalvular membrane with narrow sclerotized region on each side and they are convergent apically. Vulva membranous, narrow, connected with inner lobes of first valvulae, narrowly rounded at apex, with a narrow median longitudinal stripe. (Description of the genitalia is based on *sakuntala.*)

Winged forms: Pronotum elongate, widest behind middle, apical margin broadly rounded. Intersegmental suture between mesonotum and metanotum laterally recognized as an elevated ridge leading anteriorly to wing base. Hemelytra with vein Sc_2 connected with R + M at the point of branching into R and M.

Distribution: Oriental region (Burma, Ceylon, Southern India).

The genus *Onychotrechus* is related to *Amemboa,* but can be distinguished from it by the following more primitive characteristics:

(1) The intersegmental suture between the mesonotum and metanotum is traceable laterally.

(2) The middle and hind legs are subequal in length.
(3) The parameres are present.
(4) The suranal plate lacks modification.
(5) The apical margin of the pygophore is simple.
(6) The vein Sc_2 is united with R + M vein at the point of divergence into R and M, due to the more basal separation of R and M.

This genus is also peculiar in that the claws arise far more basally than in other genera on the extraordinarily long second tarsal segments of the middle and hind legs. The claws themselves are better developed than in the other genera of Eotrechini.

Genus *Chimarrhometra* Bianchi

(Figs. 27, 153, 572-583)

Chimarrhometra Bianchi, Ann. Mus. St. Petersbourg, p. 71(1896).
Chimarrhometra Paiva, Rec. Ind. Mus., 16(5):364(1919).

Type species: *Halobates orientalis* Distant, by original designation.

Species examined: *C. orientalis* (Distant).

Color pattern: Ferruginous in ground color. Head with basal yellow crescent shaped marking obscure. Pronotum with a median and a pair of yellow stripes.

Structures in wingless forms: Head including eyes a little wider than long, rather strongly bent ventrad anterior to eyes. Eye emarginated on inner margin. Antenna slender; first segment longest, last three segments subequal in length to one another. Antenniferous tubercles about as long as eyes. Clypeus with basal margin distinct. Mandibular and maxillary plates distinct from each other. Rostrum rather thick, extending far beyond posterior margin of prosternum; third segment about four times as long as last segment.

Pronotum with posterior margin nearly horizontal, produced laterally. Intersegmental suture between mesonotum and metanotum distinct laterally. Posterior margin of mesonotum straight. Mesonotum with a pair of well sculptured oblique grayish impressions arising from anterior margin. Mesosternum about three and a half times as long as metasternum; median longitudinal sulcus obliterated; paired longitudinal sutures absent. Metacetabular suture not extending onto dorsum. Metanotum with median longitudinal sulcus obliterated posteriorly; metanotal lateral elevation extending as far as metacetabular suture. Metasternum with omphalium located at apical one fifth of metasternum, a tuft of long hairs arising from it; omphalial groove absent. Front leg with femur strongly thickened at base, then narrowed apically; tibia curved, slightly narrowed at middle, apex with bare depression on inner margin; tarsus with first segment much shorter than second, claws arising from near apex, with fine arolium. Middle leg a little longer than hind leg; femur about one and a half times as long as tibia; tibia a little over three times as long as first tarsal segment; tarsus with first segment a little over twice as long as second tarsal segment, claws arising from very near apex. Hind leg armed with numerous black small spines as in middle leg; femur a little shorter than middle femur, a little less than twice as long as tibia; tibia over four times as long as first tarsal segment; first tarsal segment a little longer than second segment, claws arising from very near apex.

Abdomen highly reduced ventrally in male; first tergite longer than second tergite. Abdominal spiracles placed at middle of each segment; ventral longitudinal suture of connexivum absent; ventral median longitudinal impression absent.

Male: Seventh segment a little shorter than five preceding segments dorsally, or a little shorter than three preceding segments ventrally, without connexival spine, feebly sinuate on dorsal apical margin, deeply concave on ventral apical margin. Eighth segment greatly developed dorsally and with round apical margin, ventral apical margin deeply concave. Ninth segment with suranal plate mostly hidden beneath eighth tergite, slender and long, rounded on apical margin, without conspicuous modification; pygophore forked into a pair of well developed processes on apical margin; parameres greatly developed and directed ventrad apically. Endosoma with definitive dorsal plate extending along dorsal margin, loosely connected with large apical plate; lateral plates located along ventral margin near base; ventral lobe (ventral plate) small and membranous, supported by small and slender basal plate which is clearly separated from dorsal plate; apical plate directed ventrally and with broadly rounded apical margin. (Description of the genitalia is based on *orientalis.*)

Female: Female specimen was not available for study.

This genus is peculiar among the genera of Eotrechini in the following characteristics:

(1) The mesonotum is provided with a pair of oblique impressions arising from the anterior margin.

(2) A tuft of long hairs arises from the omphalium.

(3) The front femur of the male is greatly thickened.

(4) The development of the parameres and the modification of the apical margin of the pygophore are more conspicuous than in any other genus of the tribe Eotrechini.

Genus *Amemboa* Esaki

(Figs. 24, 153, 584-598, 600-601, 603-608)

Amemboa Esaki, Philip. Journ. Sci., 26(1):62(1925).
Amemboa Esaki, Ann. Mag. Nat. Hist., Ser. 10(2):508(1928).
Amemboa Lundblad, Arch. Hydrobiol. Suppl. 12, Tropische Binnengewässer, 4:405 (1933).
Amemboa Pradhan, Rec. Ind. Mus., 48(3-4):11-15(1952).

Type species: *Amemboa fumi* Esaki, by original designation.

Species examined: *A. fumi* Esaki, *A. horváthi* Esaki, *E. lyra* (Paiva), three unidentified species.

Color pattern: Reddish brown, mottled with dark to fuscous markings. Head always with median longitudinal black stripes which are confluent posteriorly, and also with a pair of black longitudinal stripes along eyes. Pronotal region with two pairs of black stripes, median pair of them are confluent anteriorly; propleural region also with two black stripes. Mesonotum with median and lateral pairs of dark fuscous stripes, each one of lateral and median pairs are connected by a transverse band. Mesopleural region with two longitudinal black stripes, silvery pubescent between them and on mesoacetabula and metacetabula. Abdomen above almost totally black to dark fuscous. General color pattern is similar to that of *Onychotrechus.*

Structures in wingless forms: Head rather strongly bent ventrad, longer than wide between eyes, uppersurface convex. Eye with inner margin slightly sinuate at middle. Antenna slender, a little shorter than body. First segment longer than second; second one usually a little shorter than third; fourth segment longest. Antenniferous tubercles inconspicuous, directed downward apically, their lateral margins slightly rounded. Clypeus with basal margin indistinct. Mandibular and maxillary plates almost completely fused, with a faint suture separating them, apical region of both sclerites always black. Rostrum relatively short, third segment a little over twice as long as last segment.

Pronotum about as long as head, wider than head including eyes, rounded on lateral and posterior margins. Intersegmental suture between mesonotum and metanotum obliterated laterally. Mesonotum with median longitudinal sulcus recognizable in posterior third or half. Mesosternum several to almost ten times as long as metasternum, feebly or not impressed on median longitudinal axis; paired longitudinal sutures absent. Metacetabular suture not reaching lateral elevation of metanotum. Metanotum with median longitudinal sulcus faintly recognizable; lateral longitudinal elevations convergent anteriorly. Metasternum with posterior margin less concave than anterior margin; omphalium distinct, located behind middle of metasternum; omphalial groove absent, remnant of lateral opening of the groove recognizable as a black spot on metacetabula. Front leg shows sexual dimorphism; femur thicker in male than in female and usually with two thick bundles of short black bristles, one near middle and another at apical one fourth of inner margin in male; tibia at basal third of inner margin always outcurved and with a bump at basal one third of inner margin in male; tarsus with first segment about half as long as second or a little shorter than second segment, claws arising from before middle of second segment, with apically curved arolium. Middle leg longer than hind leg; femur about one and a half times as long as tibia; tibia a little over twice as long as first tarsal segments; tarsus with first segment about twice as long as second segment; claws arising preapically and small. Hind leg with femur about two and a half times as long as tibia; tibia over twice as long as first tarsal segment; tarsus with first segment less than twice as long as second segment; claws arising from apical one fourth of second tarsal segment, arolium as in middle leg.

Abdomen elongate subtriangular in shape. Abdominal segments more reduced ventrally than dorsally, *flanked laterally by well developed meso- and metacetabula, so that abdominal spiracles are hidden from view. Second connexival segment often fused with third dorsally.* First abdominal tergite longer than second tergite, second to sixth tergites quadrangular in shape, of which sixth one is a little longer than the preceding one; ventrites often depressed on median longitudinal axis in male.

Male: Seventh segment ventrally well developed, a little longer than second to sixth together dorsally, ventral surface much shorter than dorsal surface, but longer than sixth ventrite. Eighth segment well developed both dorsally and ventrally, forming a cylinder-like cavity to ensheath ninth segment, dorsally about as long as seventh, ventrally a little longer than entire preceding abdominal segments together. Ninth segment with suranal plate differentiated into three regions in most species, *i. e.*, apical hairy region bearing tenth segment apically; middle region differentiates into long spinous process laterally; and lower subquadrangular plate bearing internally a process which holds upper apical region of endosoma: Pygophore modified into various shapes in various species on the apical margin; parameres lost. Endosoma with dorsal plate loosely connected with paired large round apical plates on apical margin; ventral lobe small and totally membranous, directly supported by the base of dorsal plate; lateral plates slender. (Description of the genitalia is based on *horváthi* and two unidentified species.)

Female: Seventh segment well developed both dorsally and ventrally, forming a deep cavity ensheathing genital segments, dorsally distinctly longer than sixth tergite; ventrally about as long as entire preceding abdominal segments together. Eighth segment exposed only dorsally, completely covered by seventh segment ventrally; first valvula with inner lobe simply narrowed apically, reaching middle of outer lobe; outer lobe well sclerotized on inner half, with short hairs on inner margin throughout, ramus indistinguishably fused to process of ninth tergite. Ninth segment with second valvulae sclerotized along lateral and apical margins, apical lobe small, rounded and reflexed, slightly extending beyond apical margin of intervalvular membrane which is concave. Vulva largely membranous, apical margin nearly straight except at middle, where it is sclerotized and slightly produced. (Description of the genitalia is based on *lyra.*)

Winged forms: Pronotum strongly constricted at anterior third,. forming distinct anterior and posterior lobes, posterolateral margin broadly rounded. Intersegmental suture distinct as an elevated carina connecting metathoracic spiracle and wing base. Hemelytra with veins scattered with golden hairs. Vein Sc_2 joined with R + M before the point of branching into R and M.

Distribution: Oriental region (Annam, Burma, Formosa, India, Java, Luzon, Mindanao, Sumatra.)

The genus *Amemboa* is peculiar in the Eotrechini in the following characteristics:

(1) The suranal plate is highly modified.

(2) The parameres are lost.

(3) The vein Sc_2 is united to R + M before the point of branching into R and M.

Genus *Rheumatotrechus* Kirkaldy

Rheumatotrechus Kirkaldy, Canad. Ent., 40(12):452-453(1908).

Type species: *Rheumatotrechus himalayanus* Kirkaldy, monobasic.

Specimens of the type species were not available for study. The following description is copied from Kirkaldy (1908):

"This genus has somewhat the appearance of *Ptilomera* of the Gerridae, but the legs are much shorter, especially the fore tarsi.

"Head as in *Ptilomera*, but the eyes are less oblique, and much less emarginate, the vertex being elongate, and subparallel as far as the articulation of the antennae; first segment of the antennae little longer than second; labrum much as in *Ptilomera*. In the apterous form the pronotum is well rounded at the sides, extending laterally much farther than eyes. The nota and tergites are much as in *Ptilomera*, but the whole insect is much shorter and broader in proportion, the abdominal sclerites much less elongate, the mesonotum also more rounded laterally. The fore femora are a little incrassate, and are scarcely longer than the tibiae, fore tarsi very short. Middle and hind legs much shorter than in *Ptilomera*.

"(1) *Himalayanus*, sp. nov. Pale castaneous or fulvous; head with an elongate oval mark on vertex (the interior castaneous) and some lateral marks, dark fuscous. Apex of first segment and apical fourth of second dark fuscous. Eyes dark. Last segment of labium black. Pronotum dark castaneous; a central line and lateral sinuous one on each side, yellow, the central one narrowly and rather obscurely margined with black, this spreading out a little apically. The mesonotum has a small, subtriangular, fuscous mark on each side subanteriorly. Legs yellowish-fulvous; apex of tibiae and tarsi blackish. Tergite dark castaneous, verging on piceous on abdomen proper and inward half of pleurites; one or two smaller brown spots medially. Beneath yellowish fulvous, a lateral, sinuous, dark castaneous line on the mesosternum on each side, edged with silver; also some obscure marks. The first segment of the antennae one fifth longer than the second. Fore femora scarcely longer than the tibiae, which are nearly four times as long as tarsi; last tarsal segment more than twice as long as penultimate. Middle femora slender, as long as body from base of clypeus to base of pygophor; scarcely longer than tibiae and tarsi together; tibiae about twice and a half as long as tarsi, first tarsal segment twice as long as second. Hind femora one-third longer than the middle pair; scarcely longer than the tibiae and tarsi; tibiae slightly more than twice as long as tarsi; first tarsal segment not twice as long as second. The hind part of the metanotum is triangular, the sides shortly truncate, and the base a little emarginate.

"*Male:* The pygophor is very remarkable, and I hope to figure it in my forthcoming 'Notes on the Gerridae'; the hooks, etc., are yellowish-fulvous, the apices blackish. Length—8 mm."

The genus is probably close to *Chimarrhometra* as Kirkaldy indicated by saying "This genus has considerable resemblance to *Chimarrhometra orientalis* (Distant)." The proportional lengths of the first and second tarsal segments, those of hind tibia and the hind tarsus, of the first hind tarsal segment and second tarsal segments, the remarkably modified pygophore, and the type locality lead one to strongly suspect that this genus might be a relative of *Chimarrhometra.* Hind femora being one third longer than middle pair, etc., however, definitely distinguish this genus from *Chimarrhometra.* Distant (1910) failed to locate the type specimens of this species in the Belgian Museum. I also was unable to borrow the type specimens from the same Museum where they are supposed to be preserved. The location of the types of *Rheumatotrechus himalayanus* thus remains as enigma. Although its systematic position is uncertain this genus is provisionally treated as belonging to the Eotrechini.

SUBFAMILY PTILOMERINAE BIANCHI

Ptilomerinae Esaki, Eos, Rev. Esp. Ent., 3(3):251-268(1927).
Ptilomerinae Lundblad, Ark. Zool., 27A(14):26(1927).
Ptilomerae Bianchi, Ann. Mus. Zool. Akad. Sci. St. Petersbourg, 1:74(1896).

Structures in wingless forms: Body cylindrical or oval, large in size. Head with anterior margin with three projections, median cylpeal region and lateral antenniferous tubercles in all genera except for *Rheumatogonus,* in which anterior margin is rounded. Clypeus with basal margin obliterated. Eye small and globular, its inner margin emarginated. Dorsal surface of head between eyes widened posteriorly, posterior margin feebly produced posteriorly. Antenniferous tubercles well developed and divergent except for *Rheumatogonus.* Antenna long; first segment longer than three following segments together in majority of genera; second segment longer than third or vice versa; fourth segment with apical half always curved and with a longitudinal slit. Mandibular and maxillary plates distinct from each other in all genera. Rostrum short, not extending beyond prosternum; third segment twice to three times as long as last segment.

Pronotum not prolonged, a little wider than long in most genera, lateral margins divergent anteriorly, posterior margin nearly straight or feebly concave. Intersegmental suture between mesonotum and metanotum always distinct dorsolaterally in all genera. Mesonotum without median longitudinal sulcus, with lateral longitudinal suture demarcating mesonotum from mesopleural region distinct in *Potamometra.* Mesosternum convex; paired longitudinal sutures defining mesosternum from mesopleural region distinct in some species of some genera; secondary well demarcated median flattened area extending from anterior margin of mesosternum to apical abdominal segments occurs in females of *Hetrobates.* Metanotum with or without median longitudinal sulcus; metanotal lateral longitudinal suture absent; metacetabular suture dorsally reaching anterior end of first connexival segment, dividing thus metacetabulum into anterior and posterior areas. Metathoracic spiracle conspicuous, located longitudinally. Metasternum more reduced than in Gerrinae. Omphalium reduced but present in all genera, located on median longitudinal axis of metasternum closer to posterior margin than to anterior margin; omphalial groove absent. Front leg longer than body except in *Rheumatogonus.* Femur robust, slightly narrowed apically, a little longer than tibia; tibia always with conspicuous process at inner apical angle; first tarsal segment as long as or longer than second tarsal segment; claws arising from near apex and with arolium. Middle leg longer than hind leg in all genera except for *Ptilomera* and *Potamometra; femur much longer than length of body;* with a conspicuous fringe of long hairs in males of *Ptilomera,* considerably longer and thicker than tibia; tibia with a conspicuous row of hairs in all genera; first tarsal segment several times as long as second tarsal segment; second tarsal segment with or without claws. *Hind leg with coxa more or less prolonged in some genera,* with a more or less conspicuous spinous process on apical margin in some genera; femur much longer than tibia, often three or four times as long as tibia; tibia with a row of rather short hairs on inner margin of most genera; tarsus very short, first tarsal segment shorter than second, or both segments fused, with or without claws.

Abdomen in male: First tergite with anterior margin distinct and nearly straight; second to sixth tergite subequal in length to each other in most species. Connexivum nearly horizontal or slightly reflexed, ventral longitudinal margin of connexivum distinctly recognizable as oblique suture in *Ptilomera,* obliterated or overgrown by silvery pubescence in other genera. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment in *Ptilomera,* or at middle between the margins in other genera. Seventh segment prolonged, ventral apical margin concave. Eighth segment more or less prolonged, ventral surface with a basal transversely depressed area and an obscurely elevated area in apical half in some genera, ventral apical margin concave or produced at middle. Ninth segment with suranal plate widened at middle, more or less strongly flattened, conspicuously widened apically in *Ptilomera;* pygophore more or less greatly prolonged in most genera; parameres present in all genera, simple in most genera, highly modified in *Ptilomera s. str.* Endosoma with dorsal plate never reaching apex of endosoma except for *Ptilomera* and *Potamometra*; basal plate always fused with dorsal plate; ventral plate slender and long, not bilobed and largely sclerotized.

Abdomen in female: Basal abdominal tergites more or less greatly narrowed and anterior margin of first tergite obliterated due to strong reflection of connexivum in some genera. Abdomen, except for first tergite, telescoped into thoracic cavity dorsally in *Potamometra* and *Potamometroides;* first and sixth tergites modified in some species. Abdominal spiracles and ventral longitudinal margin of connexivum as in males. Seventh segment with ventral apical margin always lobately produced, covering eighth segment above, posterolateral area also excessively developed and modified in various shapes in most genera. Eighth segment with first valvula without well differentiated inner lobe, densely clothed with long obliquely adpressed hairs on inner half of each valvula. Second valvula well sclerotized along outer margin, with well differentiated slender, well sclerotized apical processes; intervalvular membrane also with a pair of smaller processes on apical margin, always with a pair of dark spots above the processes, the spots are often confluent apically forming a single large spot; point of connection of ramus of first valvula to the process of ninth tergite distinct. Vulva largely membranous, or thinly sclerotized. First ventrite absent in both sexes.

Winged forms: Hemelytra with Sc and C distinct basally in *Ptilomera;* R + M and Cu also distinct basally in *Ptilomera, Rheumatogonus, Rhyacobates,* but fused basally in *Potamometra.* A connected with Cu at apical third of hemelytra. Pronotum with humeri located at apical third, anterior lobe well defined from posterior lobe by a transverse suture, posterior margin behind humeri broadly rounded.

Distribution: Oriental region, and one genus, *Potamometroides,* is known from Madagascar.

TABLE 12.—Table of significant generic characters in Ptilomerinae.

	Proptilomera	Ptilomera s. str.	Potamometra	Potamometroides	Potamometropsis	Heterobates	Rhyacobates	Pleciobates	Rheumatogonus
3.....	(+)	(+)	(+)	(+)	(+)	(—)	(+)	(+)	(+)
4.....	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(—)
18.....	(—)	(—)	(—)	(—)	(±)	(—)	(—)	(—)	(+)
26.....	(—)	(—)	(+)	(—)	(—)	(—)	(—)	(—)	(—)
37.....	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(+)	(+)
44.....	(+)	(+)	(—)	(—)	(+)	(+)	(+)	(+)	(+)
49.....	(+)	(+)	(+)	(+)	(+)	(—)	(+)	(+?)	(+)
50.....	(+)	(+)	(—)	(—)	(±)×	(—)	(—)	(—?)	(+)
53.....	(+)	(+)	(?)	(?)	(+)	(—)	(—)	(—)	(+)
57.....	(+)	(+)	(+)	(?)	(±)×	(+)	(+)	(+)	(+)
60.....	(+)	(—)	(—)	(—)	(±)×	(—)	(—)	(—)	(+)
63B....	(+)	(—)	(—)	(—)	(+)	(—)	(—)	(?)	(+)
68B....	(+)	(—)	(+)	(+)	(+)	(+)	(+)	(?)	(+)
69B....	(+)	(—)	(+)	(+)	(±)	(+)	(+)	(?)	(+)
71.....	(+)	(—)	(—)*	(+)	(±)	(+)	(+)	(?)	(+)
91.....	(+)	(+)	(—)	(?)	(?)	(?)	(+)	(?)	(+)
97.....	(+)	(+)	(+)	(—)	(—)	(—)	(—)	(—)	(—)
104.....	(—)	(—)	(+)	(+)	(+)	(+)	(+)	(—?)	(+)
106.....	(—)	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
111B....	(+)	(+)	(+)	(—)	(+)	(—)	(—)	(?)	(+)
112.....	(+)	(+)	(±)	(—)	(—)	(—)	(—)	(?)	(—)
113.....	(+)	(—)	(—)	(+)	(+)	(+)	(+)	(?)	(+)
114.....	(—)	(—)	(—)	(+)	(+)	(+)	(+)	(+)	(+)

TABLE 12.—Table of significant generic characters in Ptilomerinae.—*Concluded*

	Proptilomera	Ptilomera s. str.	Potamometra	Potamometroides	Potamometropsis	Heterobates	Rhyacobates	Pleciobates	Rheumatogonus
116.....	(+)	(+)	(+)	(—)	(+)	(—)	(—)	(?)	(+)
120.....	O	O	×	×	×O	O	O	(?)	O×
Total	(+)19 (±) O (—) 5 (O) 1	(+)13 (±) O (—)11 (O) 1	(+)13 (±) 1 (—) 9 (×) 1 (?) 1	(+)10 (—)11 (×) 1 (?) 3	(+)14 (±) 6 (—) 3 (×O) 1 (?) 1	(+)11 (—)12 (O) 1 (?) 1	(+)14 (—)10 (O) 1	(+) 6 (+?) 1 (—) 5 (—?) 2 (?)10	(+)20 (—) 4 (O×) 1 ....

* Pygophore is subquadrangular in shape.

For the explanations of symbols see introduction and table 5.

Relationships of genera

There appear to be three major groups of genera and two genera whose phylogenetic positions are ambigous in this subfamily.

The first group, the *Proptilomera-Ptilomera s. str.* complex, of which the latter is nothing but a more specialized group of the former, is a widely distributed group of the Ptilomerinae in the Oriental region. The peculiarities of this group are the longer hind leg than the middle leg, fused tarsal segments in the middle and hind legs although the claws are retained, the highly specialized apical abdominal segments in both sexes of the latter group, etc.

The second group is the *Rheumatogonus-Potamometropsis* group. The two genera are quite distinct, but their basically close relationship is indicated by the relatively short first antennal segment, the more nearly horizontal metacetabular suture, much less specialized apical abdominal segments in both sexes than in the other genera, etc. As noted from table 12, *Potamometropsis* and *Rheumatogonus* have more characters in common than with other genera.

The third group includes *Rhyacobates, Heterobates*, and possibly *Pleciobates*. This group is characterized by the relatively longer first antennal segment, the basally strongly reflexed connexivum, and the highly modified apical abdominal segments in the female, etc. This group is generally highly specialized as will be noted from the relatively few numbers of primitive characters, and their closely related more primitive genera are not known.

Potamometra is very similar to the *Proptilomera-Ptilomera* complex in the structures of the middle and hind legs, *i. e.*, the hind leg is longer than the middle leg, the tarsal segments being fused though the claws are retained. These characters are peculiar to these two genera in the Ptilomerinae. *Potamometra*, however, is rather drastically different from the *Proptilomera-Ptilomera s. str.* complex in certain other characters, such as the withdrawn abdomen of the female, the modified first abdominal tergite of the female, retention of the suture demarcating the mesonotum from the mesopleural region, the more specialized wing venation than in any other genera, etc. These characters preclude any possibility that this genus is closely related to *Proptilomera* or *Ptilomera s. str.* *Potamometroides* is the only African genus (Madagascar) thus far described. The genus simulate *Potamometra* in that the female abdomen is withdrawn into the thoracic cavity. In fact, however, this genus shares more characteristics in common with *Rhyacobates* or *Heterobates* than with *Potamometra.* The withdrawal of the abdomen of the female into the thoracic cavity is apparently a case of parallelism.

The above discussion is summarized roughly in the following diagram.

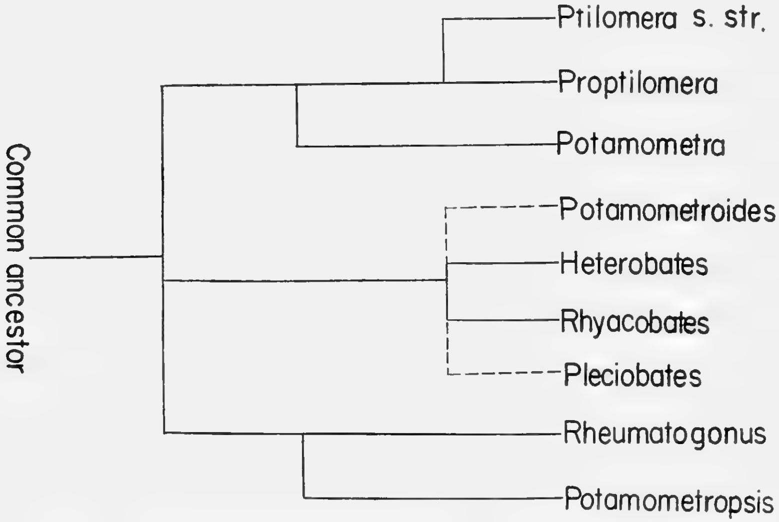

DIAGRAM 7.—Diagram showing the relationships of genera of the Ptilomerinae.

Evolutionary tendencies and characters peculiar to Ptilomerinae

The insects belonging to this subfamily always live in swift and turbulent currents. Esaki (1923) already pointed out that the extremely long first antennal segment, the long and robust femora in all legs, the presence of a fringe of hairs in the middle tibia in all genera and in the middle femur in the male of *Ptilomera* are adapted characters to this peculiar habitat. Pradhan (1952), referring to *Heterobates rihandi* (Pradhan), thinks that the triangular well demarked area on the meso- and metasterna, and abdomen in the female of the species probably helps these insects to adhere to the stones and partly submerged rocky boulders lying at the edge of water or in the bed of fast running hill streams.

In spite of these apparently adapted characters, the subfamily has certain characters which are more primitive than their counterparts in the Gerrinae, *i. e.* (1) the mandibular and maxillary plates are clearly separated from each other in all genera; (2) the primary intersegmental suture between the meso- and metanota being always distinct laterally, while it is often obliterated laterally in the Gerriniae; (3) the veins R + M and Cu being basally distinct from each other in four genera out of five investigated, while they are always fused basally in the Gerrinae.

In addition to the above-mentioned characters, the following are characteristics peculiar to this subfamily and of diagnostic importance:

(1) The metacetabular suture reaches dorsally the anterior end of the first definitive connexival segment, thus the metacetabular region is divided obliquely into the anterior and posterior halves. (In some genera of Halobatinate the metacetabular suture reaches the anterior end of the first abdominal tergite, but the metacetabular region is not divided into two laterally defined portions, since the intersegmental suture between the mesonotum and metanotum is laterally obliterated).

(2) The first connexival segment never extends into the metanotal region. (In Charmatometrini of the Gerrinae and some genera of Halobatinae the first connexival segment also does not extend into the metanotal region).

(3) The female seventh abdominal segment with the ventral apical margin is always lobately produced, and the same segment is excessively developed lateroposteriorly and variously modified. (Modification of the seventh abdominal segment of the female fre-

quently occurs in other groups of the Gerridae, but very rarely the posterolateral region of the segment is as greatly modified as in Ptilomerinae).

Genus *Ptilomera* Amyot and Serville

(Figs. 33, 36, 119-120, 137, 157, 166, 609-641)

Ptilomera Amyot and Serville, Hist. nat. insectes, Hémiptères, p. 413(1843).
Ptilomera Distant, Faun. Brit. Ind., Rhynch., 2:185(1904).
Ptilomera Esaki, Eos, Rev. Esp. Ent., 3(3):258-261(1927).
Ptilomera Lundblad, Arch. Hydrobiol. Suppl. 12:417-423(1933).
Ptilomera Hungerford and Matsuda, Bull. Brooklyn Ent. Soc., 53(5):117-123(1958) (describe Subgen. *Proptilomera*).

Type species: *Gerris laticauda* Hardwicke, by original designation.

Species examined: *P. aëllo* Breddin, *P. agriodes* Schmidt, *P. canace* Schmidt, *P. cingolensis* Stål, *P. dromas* Breddin, *P. harpalus* Schmidt, *P. harpyia* Schmidt, *P. himalayensis* Hungerford and Matsuda, *P. hylactor* Breddin, *P. lachne* Schmidt, *P. laticaudata* (Hardwicke)?, *P. pamphaga* Breddin, *P. werneri* Hungerford and Matsuda, two unidentified species.

Color pattern: General color yellowish brown to ferrugineous red, or rarely nearly black. Clypeus, apices of antenniferous tubercles black. Mesopleural region with a black longitudinal stripe or stripes clothed with short silvery pubescence. Abdominal tergites along lateral margins black and silvery pubescence. Body beneath except head almost totally silvery pubescent.

Structures in wingless forms: Male and female of about equal size. Head with anterior region not bent ventrad, widened posteriorly between eyes, posterior margin of head nearly straight. Eye small, broadly rounded on outer margin, sinuate on inner margin. Antenniferous tubercles divergent anteriorly. Antenna slender, shorter than length of body. First segment longer than three following segments together; third segment longer than second and than fourth; fourth segment curved in apical third. Rostrum not extending beyond prosternum, third segment about three times as long as last segment.

Pronotum subquadrangular in shape, about as wide as or a little wider than head including eyes, wider than long at middle, lateral margins broadly rounded, posterior margin nearly straight or feebly concave. Mesonotum about twice to two and a half times as long as pronotum, without either longitudinal sulcus or lateral longitudinal suture separating mesonotum from mesopleuron. Mesosternum with paired longitudinal sutures present in some species, less than ten times as long as metasternum in most species. Metanotum with distinct median longitudinal sulcus extending throughout entire length of metanotum; metacetabular suture strongly oblique, ventrolateral margin of metacetabulum feebly concave. Metasternum with reduced omphalium located closer to posterior margin than to anterior margin. Front leg with femur simple, a little longer than tibia; tibia with a conspicuous process at inner apical angle; apical inner surface of femur and basal inner surface of tibia with some tubercles; tarsus a little shorter than tibia; first segment about twice to a little less than three times as long as second segment; second segment thickened near apex, claws arising from near apex and with distinct arolium, without significant sexual difference in length of tarsus relative to tibia. Middle leg relatively longer in male than in female; femur in male robust, with a fringe of long hairs except in basal one fourth, femur in female bare and slender, a little less than twice as long as tibia in both sexes; tibia more or less strongly curved, with shorter fringe of hairs on inner margin in both sexes; first tarsal segment about ten times as long as second segment; second segment with small claws arising from near apex. Hind leg longer than middle leg, relatively longer in male than in female; coxa with a small spine on apical margin except for *Proptilomera*, shorter than wide; femur a little less than twice as long as tibia; both femur and tibia without fringe of hairs; first and second tarsal segments completely fused, very short, claws arising from near apex.

Abdomen long, nearly parallel-sided as far as sixth segment. Anterior margin of first tergite clearly retained, triangularly defined. anterolateral angle of the tergite elevated and with spiracle; second tergite much longer than first, second to sixth tergites subequal in length to each other, with dense mass of adpressed silvery hairs on sides. Connexivum nearly flattened or slightly reflexed. Second to sixth ventrites subequal in length. Spiracles of second to sixth segments placed closer to anterior margin than to posterior margin of each segment.

Male: Seventh segment longer than sixth segment both dorsally and ventrally, dorsal apical margin nearly straight or slightly concave, broadly concave ventrally. Eighth segment more or less greatly prolonged; ventral surface with basal transverse depression in all species and apical median longitudinal elevation in some species, ventral apical margin more or less produced posteriorly at middle. Ninth segment with suranal plate provided with more or less conspicuous process on lateral margin in most species; pygophore more or less greatly prolonged in most species, with round apical margin in most species, upper margin with a conspicuous process near middle; parameres long, curved laterally at apex, densely clothed with shaggy hairs in most species. Endosoma with dorsal plate reaching apically to apex of dorsal margin in *laticaudata*(?) and curved back along apical margin and rounded at apex in *Proptilomera;* basal plate indistinguishably fused with dorsal plate and gives support apically to slender, long and membranous ventral lobe; lateral plates absent in *Proptilomera,* but with two pairs of small lateral plates and basal dorsal region sclerotized in *laticaudata*(?). [Description of genitalia is based on *himalayensis* and *laticaudata*(?).]

Female: Seventh segment conspicuously lobately produced laterally, the lobe splits further into upper and lower lobes in *Ptilomera s. str.* Shape and degree of development of the lobes vary greatly in various species, often among individuals within the same species; ventral apical margin always lobately produced in all species, covering ventral eighth segment. First valvula along inner margin with apical cleft dividing the valvula into two lobes apically, lateral sclerotized area short, densely clothed with oblique long hairs on the area between outer margin and inner membranous region. Second valvula with lateral margin broadly sclerotized, apex directed mesad, narrowly rounded and well sclerotized; intervalvular membrane with a pair of apical processes armed with straight hairs, with a pair of oblique dark spots at bases of apical processes. [Description of the genitalia is based on *laticaudata*(?).]

Winged forms: Pronotum with anterior lobe well defined by transverse groove; humeri located at apical third of pronotum, posterior margin broadly rounded. Hemelytra with R + M and Cu veins basally distinct from each other, the two veins basally connected by a cross vein beyond middle of hemelytra. Vein A connected with Cu at about apical third of the wing. Hind leg with vein A distinct and connected with Cu at apical third of wing.

Distribution: The Oriental region (Annam, Burma, Celebes, Ceylon, China, Formosa, India, Java, Nepal, Philippines, Sumatra).

Subgenus *Ptilomera* Amyot and Serville s. str.

For type designation and citations refer to generic bibliography.

Body larger. Middle coxa with a spinous process on apical margin. Male eighth abdominal segment often with median longitudinal elevation on ventral surface; pygophore often prolonged; parameres bent apically and with a mass of shaggy hairs in many species. Female seventh abdominal segment modified posterolaterally; lobate ventral projection large.

Subgenus *Proptilomera* Hungerford and Matsuda

Proptilomera Hungerford and Matsuda, Bull. Brooklyn Ent. Soc., 53(5):117-123(1958).

Type species: *Ptilomera himalayensis* Hungerford and Matsuda.

Body relatively short. Middle coxa without spinous process on apical margin. Male eighth abdominal segment without either basal depression or longitudinal elevation on ventral surface; pygophore simply rounded on apical margin; parameres simple, without a mass of shaggy hairs apically. Female seventh abdominal segment without modification posterolaterally; lobate ventral projection small.

Modification of the abdomen and some structural characteristics

As will be noted from the above description, all the characters in *Proptilomera* are more primitive than their counterparts in *Ptilomera s. str.* From the primitive conditions in *Proptilomera,* the genital segments have become modified variously in various species as described below.

The male eighth segment: The segment has become more and more prolonged; its ventral surface has become longitudinally elevated medially in the apical half or almost entire length of the pygophore (figs. 624-628), and the ventral apical margin has become produced posteriorly at middle. The median production of the ventral apical margin also occurs in some species of *Rhyacobates.*

The male ninth segment: The suranal plate has become more and more widened apically in most species (figs. 620-623), has become widened preapically in some species. The pygophore also has become greatly prolonged and narrowed (figs. 624-629), the highest degree of prolongation is noted in *werneri* (fig. 629) from the Philippines, in which the apex is even acutely pointed; the ventral surface is greatly longitudinally elevated in *pamphagus,* and the lateral margin of the pygophore is also provided with a more or less conspicuous process basally in all species of *Ptilomera s. str.* The parameres have become clothed with a dense mass of shaggy hairs in most species, or the apex has become strongly bent in *canace* (fig. 626), or thickened and bifurcate as seen in *werneri* (fig. 629), although the parameres are quite simple and without hairs in *Proptilomera.*

The female seventh segment: The simplest modification of the upper lateral region of the segment is the production of the spinous process arising from the basal region of the seventh connexival segment only, as seen in one species from Himalaya (fig. 632); the apical lateral region has become further developed and finally the third projection (ventrolateral) has become formed in some species (figs. 634, 635). The degree of development of these lobate projections are even individually highly variable, as pointed out by Lundblad (1933).

The genus shares some peculiar characteristics in common with *Potamometra* as follows:

(1) The hind leg is longer than the middle leg.

(2) The hind tarsal segments are fused.

(3) The length of the front tarsus relative to the front tibia is without sexual difference.

Genus *Potamometra* Bianchi

(Figs. 28, 119-120, 642-655)

Potamometra Bianchi, Ann. Mus. Zool. Acad. Sci. St. Petersbourg, p. 71 (1896).
Potamometra Esaki, Eos, 2(3):254(1927).
Potamometra Lundblad, Ark. Zool., 27 A(14):26(1934).
Thaumastometra Kirkaldy, Rev. d'Ent., 18:86(1899) (type species, *Thaumastametra montandoni* Kirkaldy).

Type species: *Potamometra berezowskii* Bianchi, by original designation.

Species examined: *P. Berezowskii* Bianchi, *P. tibetensis* Esaki.

Color pattern: Predominantly black in ground color. A median yellow longitudinal stripe from middle of head down to metanotum, short yellow hairs rather densely scattered on black ground color giving a grayish tinge, silvery adpressed hairs distributed on pleural regions of all three thoracic segments, thus giving an appearance of a broad white band on each side of the body. Legs yellow with black stripes, apical regions on femora of all legs pale yellow.

Structures in wingless forms: Large and broad, with extremely long legs. Head somewhat obliquely directed anteriorly, strongly widened posteriorly between eyes, posterior margin nearly straight. Antenniferous tubercules divergent apically. Eye globular and small, inner margin strongly concave. Antenna shorter than length of body; first segment longer than three following segments together, relative length of second to first greater in female than in male; fourth segment shortest. Rostrum rather slender, third segment over twice as long as last segment.

Pronotum with lateral margin broadly rounded or convergent anteriorly, wider than head including eyes, posterior margin feebly sinuate on either side of middle or nearly straight. Mesonotum laterally well defined from mesopleural region by a longitudinal suture from behind posterolateral angle of pronotum to intersegmental suture between mesonotum and metanotum. Mesosternum less than ten times as long as metasternum, about three times as long as second abdominal ventrite in male. Metanotum without distinct median longitudinal sulcus; metacetabular suture strongly oblique dorsally. Metasternum relatively longer in male than in female; omphalium placed midway between anterior and posterior margins of metasternum. Front legs longer than body. Femur about one and one sixth times as long as tibia, thick, with numerous small black tubercles on inner margin; tibia with process on inner apical angle conspicuous; tarsus about as long as tibia in both sexes, first segment over three times as long as second; second segment thickened apically, claws arising from near apex, with fine arolium. *Middle leg with femur almost twice as long as total length of body,* over one and a half times as long as tibia, without hairs on inner margin; tibia with a fringe of long hairs on inner margin except in basal and apical regions, a little less than twice as long as first tarsal segment; first tarsal segment over ten times as long as second segment; second tarsal segment with small claws. Hind legs longer than middle leg; coxa about as long as wide, with a process at inner apical angle projecting posteriorly, the process much more developed in female than in male; femur longer than middle femur, a little less than one and a half times as long as tibia; first and second tarsal segments fused, with small claws arising from near apex.

Abdomen in male: First abdominal tergite very short, its anterior margin distinct; second to sixth tergites inclined posteriorly, seventh tergite sometimes folded beneath the preceding segment. Connexival segments nearly vertically reflexed, second to sixth ventrites strongly reduced, seventh segment ventrally greatly developed and much longer than all preceding segments together. Eighth segment greatly prolonged, cylindrical, lifted upward apically (thus in fig. 643 dorsal apical margin looks concave). Ninth segment with suranal plate roundly produced at middle of lateral margin, apex rounded; pygophore well exposed, subquadrangular in shape and a little shorter than preceding segment, apical margin slightly produced, with a dark process arising on lateral margin anterior to the base of parameres; parameres long, protruded beyond apex of pygophore. Endosoma with dorsal plate slender, reaching apex of endosoma, basally indistinguishably fused with basal plate, this in turn bears dark slender thread like ventral plate; lateral plates simple and long. (Description of the genitalia is based on *berezowskii*).

Abdomen in female: First tergite with anterior margin concave at middle, produced posteriorly as a long process at middle; tergites from second segment on folded to be telescoped into thoracic cavity; ventrally only four basal segments are exposed, the rest telescoped into thoracic cavity. First valvula broad, inner region membranous, a dense mass of straight adpressed hairs located lateral to inner membranous region, long and narrow sclerotized area lateral to the haired area reaching apex of valvula; ramus robust. Second valvula with lateral sclerotized area tapering apically, apex directed posteromesially, rather thick, sclerotized except at extreme apex, broadly rounded; paired processes on apical margin of intervalvular membrane sparsely bearing straight hairs, with a pair of oblique slender sclerotized pieces basal to the processes. (Description of the genitalia is based on *berezowskii.*)

Winged forms: Pronotum with humeri located at apical one third, posterior margin broadly rounded. Forewing with R + M and Cu fused basally as in typical gerrinae, but Sc_2 not connecting Sc and R + M. Hind wing with A reaching to Cu beyond the middle of wing.

Distribution: China.

The genus *Potamometra* is peculiar in the following points, which set this genus off from all other genera of the subfamily:

(1) The mesonotum is provided with the lateral longitudinal sutures defining the mesopleura laterally.

(2) The first abdominal tergite of the female has a conspicuous median projection; the same in the male is very short.

(3) The pygophore is subquadrangular in shape.

Genus *Rhyacobates* Esaki

(Figs. 29, 119-120, 656-680)

Rhyacobates Esaki, Philip. Jour. Sci., 22(4):367-388(1923).
Rhyacobates Esaki, Eos, 3(3):254(1927).
Rhyacobates Lundblad, Ark. Zool., 27A:26(1934).
Rhyacobates Hungerford and Matsuda, Jour. Kansas Ent. Soc., 32(2):69-72 (1959) (*Esakobates* synonymized with *Rhyacobates*).
Esakobates Lundblad, Ark. Zool., 27A:22-26(1934) (type species, *Esakobates svehedini* Lundblad).

Type species: *Rhyacobates takahashii* Esaki, by original designation.

Species examined: *R. takahashii* Esaki, *R. chinesis* Hungerford and Matsuda, *R. lundbladi* (Hungerford), *R. svehedini* (Lundblad).

Color pattern: Predominantly black dorsally. Head with a median black spot and marginal yellowish brown area. Pronotum black, with a median yellowish brown spot, marginal area of pronotum in winged forms yellowish brown. Mesonotum black, with silvery pubescence, median longitudinal yellowish brown stripe not reaching anterior margin. Legs yellowish brown. Abdomen with connexivum pale yellowish brown or black and silvery pubescent. Meso- and metacetabular regions yellowish brown, silvery pubescent.

Structures in wingless forms: Female much larger than male. Head with anterior margin not bent ventrad, widened posteriorly between eyes. Antenniferous tubercles divergent anteriorly, obtuse at tips. Antenna with first segment longer than three following segments together; second segment subequal to or shorter than third; fourth segment curved in apical half, shortest. Rostrum short, not extending beyond prosternum; third segment over twice as long as last segment.

Pronotum transverse, subquadrangular in shape, lateral margins divergent anteriorly, posterior margin feebly sinuate or nearly straight. Mesonotum about three times as long as pronotum in males, over three times as long as pronotum in females, without lateral longitudinal suture separating mesonotum from mesopleural regions. Mesosternum about ten times as long as metasternum; paired longitudinal sutures sometimes present. Metanotum with median longitudinal sulcus distinct throughout entire length of metanotum; metacetabular suture strongly oblique dorsally. Metasternum with reduced omphalium located at a little behind middle. Front leg longer than body. Femur robust, slightly tapering apically, longer than tibia with inner apical process more or less conspicuous in both sexes; first tarsal segment about one third as long as tibia in male, or a little over half as long as tibia in female, one and three fifths to almost twice as long as second tarsal segment in male, over twice as long as second in female; claws arising from near apex, robust, with hair like arolium arising from base of claws. Middle leg with femur about twice or a little less than twice as long as tibia in both sexes, without dense fringe of long hairs on inner margin; tibia with a row of short hairs on entire inner margin; first tarsal segment several times as long as second tarsal segment, strongly curved; second tarsal segment without claws. Hind leg shorter than middle leg; coxa longer than wide, without spine on apical margin; femur a little longer than middle femur, about two and a half to three and a half times as long as tibia; tibia with a row of shorter hairs on inner margin; first tarsal segment a little shorter than second tarsal segment; second segment without claws. Abdomen with anterior margin of first tergite slightly produced anteriorly, with a more elevated subtriangularly defined area laterally, each enclosing first abdominal spiracle within; first to sixth tergites in male transverse, seventh tergite subquadrangular, about twice as long as sixth in male. Connexivum in female strongly reflexed, lateral margins often meet each other above tergites in females, ventrites progressively longer posteriorly. Abdominal spiracles on third to sixth segments placed a little closer to anterior margin than to posterior margin.

Male: Seventh segment about one and a half times as long as sixth ventrally. Eighth segment with ventral apical margin slightly produced posteriorly, densely clothed with long hairs; ventral surface transversely depressed basally, longitudinally elevated in middle of apical half. Ninth segment with suranal plate widened in apical half, basal lateral angle with a foot shaped process; pygophore well exposed, rounded on apical margin; parameres simply curved and slender. Endosoma with dorsal plate not reaching middle of endosoma, bifurcate apically, indistinguishably fused with basal plate, which in turn gives support to long and slender ventral lobe, without either well defined lateral plates or apical plate; ventral margin of endosoma more or less sclerotized. (Description of the genitalia is based on *lundbladi* and *takahashii).*

Female: Seventh segment ventrally about twice or over twice as long as sixth, posterior margin bisinuate, with an inconspicuous median projection; connexivum with posterolateral region of seventh segment modified as shown in figures 671, 673, 676. Eighth segment with first valvula membranous, with or without a small spinous process on inner margin near apex, ventral surface densely clothed with long and straight hairs which are obliquely adpressed, apex narrowly rounded, outer margin sclerotized. Second valvula with lateral margin broadly sclerotized, apex narrowly rounded; intervalvular membrane with a pair of small haired sclerotized processes on apical margin, with dark spots above the processes on intervalvular membrane.

Winged forms: Pronotum with humeri located much behind middle, broadly rounded behind humeri. Tergites in *lundbladi* much like in wingless forms of the same species. Wing venation (Esaki, 1925) as in *Ptilomera* and *Rheumatogonus.* R + M and Cu veins are basally separated and they are connected by a cross vein.

Distribution: The Oriental region (Formosa, Southern China).

Genus *Heterobates* Bianchi

(Figs. 31, 119-120, 681-701)

Heterobates Bianchi, Ann. Mus. St. Petersbourg, p. 74(1896).
Heterobates Esaki, Eos, 3(3):254(1927).
Heterobates Hungerford and Matsuda, Ent. News, 69(8):200-201(1958) (*Teratobates,* a synonym of *Heterobates*).
Teratobates Esaki, Eos, Rev. Esp. Ent., 3(3):254, 261-262(1927) (type species, *Teratobates bilobatus* Esaki).
Teratobates Pradhan. Rec. Ind. Mus., 48:101-105(1950).

Type species: *Heterobates dohrandti* Bianchi, by original designation.

Species examined: *H. dohrandti* Bianchi, *H. bilobatus* (Esaki).

Color pattern: Black in ground color, clothed with short silvery pubescence dorsally. Head with a median black spot and marginal ochraceous area. Pronotum with or without median longitudinal ochraceous stripe. Mesonotum with a median longitudinal ochraceous stripe. Proacetabular region, coxae and trochanters of all legs ochraceous. Abdomen beneath and mesosternum along median longitudinal axis ochraceous.

Structures in wingless forms: Head not bent ventrad, widened posteriorly between eyes. Antenniferous tubercles divergent anteriorly. Antenna about as long as body in male, considerably shorter than body in female. First segment longer than three following segments together; second segment longer than third; fourth segment shortest, curved in apical half. Rostrum thick and densely clothed with gray hairs; third segment over twice as long as last segment.

Pronotum a little wider than head including eyes, posterior margin feebly concave but feebly produced medially, lateral margins slightly divergent anteriorly. Mesonotum about three times as long as pronotum in male, about four times as long as pronotum in female. Mesosternum about ten times as long as metasternum, without longitudinal suture separating mesonotum from mesopleural region; *with distinctly demarcated median flattened area extending the entire surface of mesosternum and further onto apical abdominal segments in female.* Metanotum has distinct median longitudinal sulcus. Metacetabular suture dorsally strongly oblique. Metasternum with highly reduced omphalium located closer to posterior margin than to anterior margin of metasternum. Front leg with femur sparsely clothed with long hairs on inner margin, about one and one fifth times as long as tibia; tibia with a conspicuous process at inner apical angle; tarsus a little over half as long as tibia in male, or about two thirds as long as tibia in female; first tarsal segment about one and a half to about twice as long as second segment; second segment with claws arising from apical one fourth and with membranous arolium which is apically curled. Middle leg with femur longer than body, relative length of femur to body greater in male than in female, a little over twice as long as tibia; tibia with fringe of rather conspicuous hairs in both sexes; tarsus strongly curled and flattened; first segment several times as long as second, fringed with hairs in basal one fourth; second segment without claws. Hind leg shorter than middle leg. Coxa longer than wide, without spine on apical margin; femur over four times as long as tibia; tibia strongly curved apically, with inconspicuous fringe of hairs on entire inner margin; first tarsal segment shorter than second segment; second segment without claws.

Abdomen in male: Anterior margin of first tergite recognizable, produced anteromesially, first abdominal spiracle clearly recognizable, anterior margin of second tergite produced anteriorly; third to fifth subequal in length; sixth a little longer than fifth; ventrally second to sixth subequal in length; seventh a little longer than sixth, its posterior margin broadly concave. Eighth segment with dorsal apical margin rounded, slightly produced posteromesially on ventral apical margin. Ninth segment with suranal plate widened preapically and flattened laterally; pygophore well exposed, narrowly rounded on apical margin; parameres well exposed, slender and long, narrowly rounded on apical margin. Endosoma with dorsal plate hook-shaped, bent obliquely cephalad apically, extending beyond middle of endosoma, indistinguishably fused with basal plate, which in turn is fused with narrower ventral plate; ventral plate membranous apically; lateral plates oblique, located basally; apical plates connected posteriorly to each other by a narrow transverse bridge, the bridge in turn connected with apex of dorsal plate. (Description of the genitalia is based on *dohrandti*).

Abdomen in female: Basal tergites obliterated due to reflection of connexivum. Connexivum slanting towards middle basally, exposed area of tergites triangular, each tergite becoming progressively larger posteriorly, posterolateral angle of sixth connexival segment subrectangularly produced inward; spiracles of second to sixth ventrites placed at middle of each segment. Seventh segment broadly rounded on dorsal apical margin, lobately produced laterally, with rather acute or broadly rounded apex, ventral lobate apical margin straight, totally or not totally covering eighth segment above. Eighth segment with dorsal apical margin broadly rounded. First valvula with inner half largely membranous and densely clothed with straight, long and adpressed hairs which are directed caudad, apex sclerotized and narrowly rounded, outer margin well sclerotized; ramus robust, arising from beyond apex of lateral well sclerotized area. Second valvulae with outer margin broadly rounded, membranous near apex, apices directed mesad and rounded; intervalvular membrane with two small membranous processes bearing hairs on apical margin, black spot at bases of processes obliterated. (Description of the genitalia is based on *dohrandti.*)

Distribution: Nepal, Northern India, Turkestan.

This genus is closely related to *Rhyacobates,* but differs by the following characteristics:

(1) The ventral side of the body with distinctly demarcated area extending from the mesosternum to the apical abdominal segments in the female.

(2) The hind femur is over four times as long as tibia; it is less than three and a half times as long as tibia in *Rhyacobates.*

(3) The middle femur is over twice as long as the middle tibia; it is less than twice as long as tibia in *Rhyacobates.*

(4) The second antennal segment is always longer than the third; the second is as long as or shorter than third in *Rhyacobates.*

(5) The anterolateral angle of the mesonotum is somewhat produced.

Genus *Potamometroides* Hungerford

(Figs. 35, 119-120, 702-712)

Potamometroides Hungerford, Jour. Kansas Ent. Soc., 24(4):131-133(1951).

Type species: *Potamometroides madagascariensis* Hungerford, by original designation.

Species examined: *P. madagascariensis* Hungerford.

Color pattern: Body above predominantly black. Head with a black spot continuous with black marginal area along eyes. Clypeus and basal region of head yellowish brown. Pronotum black, with median yellowish brown stripe. Mesonotum totally black, with lateral longitudinal stripes composed of silvery pubescence reaching posteriorly to metathoracic spiracle. Abdomen entirely black above, pro-, meso- and metapleural regions yellowish brown. Meso- and metasternal regions black. Legs yellowish brown to nearly black.

Structures in wingless forms: Head not bent anteriorly, strongly widened posteriorly between eyes, posterior margin nearly straight or feebly concave. Antenniferous tubercles divergent anteriorly. Antenna a little longer than length of body in male; first segment longer than three following segments together; second segment as long as third; fourth segment curved and shortest. Rostrum not extending beyond prosternum; third segment twice as long as last segment.

Pronotum widened anteriorly, wider than head including eyes, posterior margin of head produced posteriorly at middle in female, nearly straight in male. Mesonotum about three times as long as pronotum in both sexes, without lateral longitudinal suture separating mesonotum from mesopleuron, posterior margin concave dorsally. Mesosternum over ten times as long as metasternum. Metanotum without median longitudinal sulcus. Metacetabular suture dorsally strongly oblique. A long process arising from dorsal apical angle of mesoacetabulum superposed on metacoxa in female. Metasternum with reduced omphalium, posterior margin less concave in female than in male. Front leg with femur one and one fifth to one and one sixth times as long as tibia; sparsely clothed with long straight hairs on inner margin; tibia with inner apical process conspicuous, twice as long as first tarsal segment in female, three times as long as first tarsal segment in male; first tarsal segment a little less than twice as long as second segment; second tarsal segment with claws arising from near apex, claws with slender membranous arolium. Middle leg with coxa rather short; femur a little less than twice as long as tibia, without fringe of hairs; tibia with fringe of long hairs on inner margin, narrowed apically; first tarsal segment strongly curved, about five times as long as second; second segment without distinguishable claws. Hind leg shorter than middle leg; coxa about three times as long as wide, slightly narrowed apically; femur relatively longer in male than in female, about four times as long as tibia in male, about three times as long as tibia in female; first tarsal segment a little shorter than second segment; second segment without claws.

Abdomen in male: Shorter than mesonotum and metanotum together. First tergite with anterior margin distinct, obliquely ridged laterally; second tergite with anterior margin broadly produced, long; third to fifth tergites subequal in length; sixth tergite longer than fifth; seventh tergite much longer than sixth, broadly rounded on apical margin; second to sixth ventrites greatly reduced; seventh segment ventrally over twice as long as sixth at middle and broadly concave on apical margin. Eighth segment greatly prolonged and cylindrical, convex on dorsal apical margin and nearly straight on ventral apical margin. Ninth segment with lateral projection not conspicuous; pygophore well exposed, rather strongly narrowed apically, apical margin rounded; parameres well developed. Endosoma with dorsal plate indistinguishably fused with basal plate, thinly sclerotized, boot-shaped process on ventral margin of dorsal plate, reaching middle of endosoma; ventral plate fused with basal plate at basal ventral angle of endosoma, broad and strongly sclerotized, membranous and lobate apically, ventral margin of endosoma lobately produced apically, without well defined lateral plate. (Description of the genitalia is based on *madagascariensis.*)

Female: Abdomen, leaving first tergite dorsally and second ventrite ventrally, completely telescoped into thoracic cavity. First tergite as in male; seventh ventrite simply elongate and with feebly concave apical margin. First valvula densely clothed with straight adpressed hairs directed caudad on inner half, apex narrowly rounded, sclerotized in apical region, upper lateral margin sclerotized; ramus attached to the process of ninth tergite at apex. Second valvula with lateral margins well pigmented, apical well sclerotized process located mesal to apical end of sclerotized lateral margin; ramus fine, arising from near apex of lateral margin of second valvula, basally reaching apex of process of ninth tergite; intervalvular membrane with a pair of small processes, sparsely clothed with hairs on apical region of intervalvular membrane, crescent shaped spot above base of apical processes of intervalvular membrane. (Description of the genitalia is based on *madagascariensis.*)

Distribution: The Ethiopian region (Madagascar).

The genus *Potamometroides* and *Potamometra* are the only genera in which the abdomen of the female is telescoped into the thoracic cavity. This, however, does not suggest any close relationship between the two genera. As already noted elsewhere, *Potamometra* shares a few peculiar characteristics in common with *Ptilomera,* and it has three peculiar characters which set this genus off from all the other genera. The withdrawal of the abdomen in the female of these two genera is apparently a case of parallelism. It is interesting also to point out that a well-developed conspicuous process occurs on the posterior margin of the first tergite and at the inner apical angle of the hind coxa in the female of *Potamometra,* while a similar process occurs at the inner apical angle of the metacetabulum in the female of *Potamometroides.*

Genus *Potamometropsis* Lundblad

(Figs. 30, 119-120, 713-731)

Potamometropsis Lundblad, Arch. Hydrobiol. Suppl. 12, 4:415(1933).
Potamometropsis Hungerford, Jour. Kansas Ent. Soc., 30(4):125-130(1957).

Type species: *Potamometropsis obnubila* Lundblad, by original designation.

Species examined: *P. hoogstraali* Hungerford, *P. obnubila* Lundblad, *P. werneri* Hungerford.

Color pattern: Uppersurface predominantly black and silvery pubescent. Head with a large black spot on centre, yellowish brown marginally. Pronotum with median yellowish spot or stripe. Mesonotum with or without yellowish brown spots, with lateral silvery stripe from anterior margin to metathoracic spiracle. Abdomen above black except for connexivum of *P. hoogstraali* which is yellowish brown. Body beneath largely yellowish brown, silvery pubescent throughout the entire surface.

Structures in wingless forms: Head not bent anteriorly, slightly widened posteriorly between eyes, much narrower than anterior region, posterior margin of head concave. Antenniferous tubercles divergent anteriorly. Antenna a little shorter than length of body. First segment about as long as three following segments together; second segment shorter than third segment; relative length of second to third is a little greater in male than in female; third segment truncate at apex; fourth segment shorter than third, curved at middle. Rostrum not extending beyond prosternum; third segment a little over twice to about three times as long as last segment.

Pronotum wider than head including eyes, lateral margin broadly rounded, posterior margin either concave or convex. Mesonotum about two and a half times as long as pronotum, relatively a little longer in female, posterior margin of mesonotum feebly concave at middle; lateral longitudinal suture separating mesonotum from mesopleuron absent. Metanotum with median longitudinal sulcus obsolete; metacetabular suture dorsally gently oblique, nearly horizontal. Metasternum with vestigial omphalium located close to posterior margin. Front leg with femur one and one fourth to one and one third times as long as tibia, a little thicker in male than in female; tibia with inner apical process more conspicuous in female than in male; first tarsal segment less than twice as long as second, second segment with claws arising from near apex, claws with arolium. Middle leg with coxa short; femur straight, much longer than length of body, a little less than twice as long as tibia, without fringe of hairs on inner margin; tibia strongly curved and with fringe of long hairs throughout entire inner margin in both sexes; first tarsal segment between three and four times as long as second segment; second segment with distinct claws arising from near apex. Hind leg shorter than middle leg; coxa a little longer than wide; femur between two and three and a half times as long as tibia; tibia fringed with hairs throughout the entire inner margin; first tarsal segment much shorter than second segment; second segment with distinct claws.

Abdomen with anterior margin of first tergite distinct, first tergite with median elevation arising from anterior margin in female of *werneri;* sixth tergite with median apical production in female of *hoogstraali.* Connexivum either flattened horizontally or subvertically erected, apical angle of sixth connexival segment strongly produced in female of *hoogstraali;* second ventral segment much shorter than metasternum; second to sixth ventrites subequal in length. Abdominal spiracles of second to sixth segments located at about middle of each segment.

Male: Seventh segment dorsally over twice as long as sixth tergite, ventral apical margin broadly concave, also over twice as long as sixth ventrite. Eighth segment strongly produced except for *hoogstraali,* its dorsal apical margin broadly rounded. Ninth segment with suranal plate simply widened preapically; pygophore well exposed and long; parameres conspicuous and long. Endosoma with dorsal plate hook-shaped, apex directed obliquely cephalad, thinly pigmented and completely fused with thick and dark basal plate, which in turn gives support to ventral lobe; ventral lobe largely membranous; lateral plates obliquely placed. (Description of the genitalia is based on *hoogstraali*).

Female: Seventh segment ventrally excessively developed, and ventral apical region greatly varies in shape in various species. Eighth segment ventrally completely covered by apical region of seventh ventrite except for *obnubila,* in which seventh segment is least prolonged and eighth segment apically exposed ventrally. First valvula broad, inner half densely clothed with long straight hairs directed caudad, with sclerotized area lateral to inner haired area, apex narrowly rounded; ramus reaching apical third of valvula. Second valvula with lateral margin broadly sclerotized, apical lobe directed posteromesially, broadly rounded apically; intervalvular membrane with a pair of small apical processes bearing straight hairs, with strongly pigmented U-shaped spot above apical margin; ramus slender, arising from near apex of second valvula, not much extending caudad along lateral margin of the valvula. (Description of the genitalia is based on *hoogstraali.*)

Distribution: The Oriental region (Sumatra, Philippines).

The genus *Potamometropsis* shares two important characters in common with *Rheumatogonus, i. e.,* the nearly horizontal metacetabular suture and the absence of the modification of the posterolateral region of the seventh abdominal segment of the female. They are probably more closely related to each other than to others, but *Potamometropsis* differs from *Rheumatogonus* in the anterior margin of the head which is not rounded and in the first antennal segment which is relatively longer.

Genus *Rheumatogonus* Kirkaldy

(Figs. 32, 119-120, 127, 732-747)

Rheumatogonus Kirkaldy, Canad. Ent., 41:390(1909) (as subgenus of *Ptilomera*).
Rheumatogonus Esaki, Eos, Rev. Esp. Ent., 3(3):265(1927).
Jucundus Distant, Ann. Mag. Nat. Hist., 5(8):145(1910) (type species, *Jucundus custodiendus* Distant).

Type species: *Ptilomera luzonicus* Kirkaldy, monobasic.

Species examined: *R. burmanus* (Distant), *R. intermedius* Hungerford.

Color pattern: Predominantly yellowish brown, tergites fuscous to nearly black, or sometimes yellowish brown. Metanotum with median black longitudinal stripe in *intermedius.*

Structures in wingless forms: Relatively small in size and cylindrical in shape. Head with anterior region of head strongly bent ventrad and anterior margin broadly rounded, widened posteriorly between eyes, posterior margin of head nearly straight. Eye large and long, exserted. Antenniferous tubercles with cavities open ventrad. Antenna considerably shorter than length of body; first segment considerably shorter than three following segments together; second segment equal to or longer than third; fourth segment shorter than third, slightly curved in apical third. Rostrum not extending beyond prosternum; third segment with paired long hairs near apex on dorsal surface, a little over twice to three times as long as last segment.

Pronotum with lateral margins divergent anteriorly or rounded, about as wide as head including eyes, posterior margin slightly sinuate on either side of middle. Mesonotum with dorsal posterior margin feebly concave, its relative length to pronotum a little over twice as long as pronotum in male, over two and a half times as long as pronotum in female. Mesosternum with posterior margin slightly concave, about ten times as long as metasternum. Metanotum with median longitudinal sulcus not recognizable in *intermedius,* normally distinct in *burmanus,* lateral longitudinal suture separating mesonotum from mesopleuron absent; metacetabular suture dorsally nearly horizontal. Metasternum with omphalium inconspicuous, located at apical third of metasternum. Front leg a little shorter than body; femur one and one third to one and a half times as long as tibia, sparsely clothed with dark hairs on inner margin; tibia gradually thickened apically, inner apical process not conspicuous; relative length of tarsus to tibia considerably greater in female than in male, ranging from one and seven tenths to two and one third times as long as tibia; first tarsal segment as long as or shorter than second in male, or a little longer than second in female, claws arising from apical third of second segment. Middle leg with coxa short; femur less than twice as long as tibia, without fringe of hairs; tibia curved, about three times as long as first tarsal segment; first tarsal segment four to five times as long as second, both segments highly curved, second one with distinct claws. Hind leg shorter than middle leg; coxa a little longer than wide; femur about three times as long as tibia; tibia about ten times as long as tarsus, strongly curved apically; first tarsal segment a little shorter than second segment, which is without claws.

Abdomen with anterior margin of first tergite distinct, feebly convex, with anterolateral subtriangularly defined area enclosing spiracle, short; second tergite about as long as wide, much longer than either first or third tergite; third to sixth tergites subequal in length, narrowed apically. Connexivum more or less reflexed, neither greatly modified nor folded on dorsum. Abdominal spiracles of second to sixth ventrites placed at middle of each segment.

Male: Seventh segment about twice as long as sixth segment both dorsally and ventrally, broadly rounded on dorsal apical margin and concave on ventral apical margin. Eighth segment more or less greatly prolonged, telescoping basal ninth segment within. Ninth segment with lateral production of suranal plate not conspicuous; pygophore well exposed, broadly rounded on apical margin; parameres well developed, simply curved upward and tapered apically. Endosoma membranous, dorsal plate thinly sclerotized and short, basally fused with strongly sclerotized oblique and robust basal plate, which bears apically slender, short and membranous ventral plate; without well-defined lateral plates. (Description of the genitalia is based on *intermedius.*)

Female: Seventh segment greatly prolonged, ventrally with median lobate process covering eighth segment, laterally simply acutely pointed, dorsally nearly straight on apical margin. Eighth segment with first valvula rather narrow, long adpressed hairs relatively scarce, apex obtusely rounded; ramus rather slender, attached to outer apical angle of process from ninth tergite. Second valvula with lateral margin broadly sclerotized; ramus fine, apical process arising mesal to apical region of the valvula, narrow and long, directed more or less mesad, apical paired processes of intervalvular membrane without conspicuous mass of hairs, with an inversed V-shaped spot above base of apical processes of intervalvular membrane. (Description of the genitalia is based on *intermedius.*)

Winged forms: Pronotum widest at apical one third, broadly rounded on apical margin. Hemelytra with R + M and Cu are connected by a cross vein at basal one fourth; Cu and A are united at a little beyond middle of hemelytron.

The genus *Rheumatogonus* is specialized in that the anterior margin of the head is strongly bent ventrad, but it is more primitive than any other genera in that the first antennal segment and the femora of all legs are relatively much shorter than in other genera, in other words, they have not been as greatly prolonged as in other genera in adaptation to their peculiar habitat (swift and turbulent currents). Another primitive feature is that the seventh abdominal segment of the female is not modified on the posterolateral area.

Genus *Pleciobates* Esaki

Pleciobates Esaki, Jour. Fed. Malay Mus., 16(1-2):13-14(1930).

Type species: *Pleciobates tuberculatus* Esaki, by original designation.

The specimens of this genus have not been available for study. The following is the original description by Esaki:

"*Apterous form; female:* Body oblong, fusiform. Head much longer than broad between eyes, anteocular portion not longer than the rest of head. Eyes much rounded laterally, slightly emarginate interiorly. Antennae very long and slender, not longer than body, first segment longer than the rest of antennae, second and fourth segments subequal in length, third one-third the length of first, a little longer than the second. Rostrum not passing the anterior coxae, third segment much the longest, a little swollen at middle. Pronotum transverse, anterior and posterior margins nearly straight. Mesonotum very large, three times as long as pronotum, lateral margins not quite parallel. Metanotum much shorter than mesonotum, a little longer than pronotum, lateral portions more or less confluent with mesothorax, *separated into two portions antero-posteriorly, posterior portion much shorter than the anterior portion.* Anterior legs slender, femur stoutest, slightly tapering towards the apex, tibia more slender and shorter than femur with an acute process at the inner side of apex, tarsus much longer than half the length of tibia, first segment one and a half times as long as second. Intermediate and posterior legs very long and slender; intermediate femur much longer than body; tibia more slender than femur, a little longer than half of the latter; tarsus about one half of tibia, much thinner than tibia, tapering towards the apex, first segment about six times as long as second; posterior femur slightly shorter and much thinner than intermediate femur, tibia about a half of femur tapering towards the apex, tarsus very short, not longer than one tenth of tibia, first segment about twice the length of the second. Intermediate and posterior acetabula lateral to the abdomen. Abdomen broad and short, about as long as mesonotum. Dorsal segments very broad, first four segments subequal in length, fifth longer than the two preceding segments together, sixth shorter than the fifth. Ventral segments ring-shaped, first five segments equal in breadth, the sixth much narrower, more or less tube-like. Female genital segments very small, slightly protruding the end of abdominal segment. Connexivum broad, almost perpendicularly erected, ending into a very long, stout spine-like process, which is much projecting beyond the end of abdominal segment.

"Male and the macropterous form unknown.

"Type: *Pleciobates tuberculatus* sp. nov.

"This genus undoubtedly belongs to the subfamily *Ptilomerinae*. It differs from the other genera of the subfamily in the shorter head, very remarkable structure of the connexivum, and in some other less important characters. The female of *Ptilomera* Amyot et Serville have an apparently similar structure of the connexivum to that in this genus, but in the former the apical prolongation is rather filament-like, whereas in the latter the same is stout and spine-like. As a matter of fact this genus is more closely allied to *Rhyacobates* Esaki, than to *Ptilomera* Amyot et Serville.

"*Pleciobates tuberculatus* sp. nov.

"*Apterous female:* Body black with brown markings, and grayish pubescence. Head dark brown, a large middle spot on the anterior part of vertex, basal margin of head, antenniferous tubercles, extreme apex of frons black, with minute brown pubescence. Eyes black, shining. Antennae totally black. Rostrum very pilose, dark brown with the apical half of the third and the entire fourth segment black. Dorsal surface of thorax pitchy black, more or less shining, a conspicuous longitudinal brown marking in the middle of pronotum; lateral sides, suture between meso- and metanotum and a small area on each side of the median longitudinal line of mesonotum with silvery, grayish pubescence. Prosternum pale brown with the same coloured pubescence, with a very small black spot at the end of the acetabular suture. Mesosternum black, except the posterior area and acetabulum which are pale brown, with very dense grayish pubescence. Metasternum (apparently the first ventral abdominal segment) pale brown, thickly pubescent. Anterior coxa, trochanter and femur brown, extreme base and apex of femur, three conspicuous stripes on the femur, tibia and tarsus black. Intermediate and posterior legs black with the coxae, trochanters and the base of the intermediate femur brown. Dorsal surface of abdomen pitchy black, coarsely covered with grayish pubescence, apex of the last genital segment brown. Connexivum pitchy black with the apical prolonged portion pale brown. Ventral surface of abdomen pale brown, sixth segment much darker; thickly covered with silvery grayish pubescence.

"Body fusiform, about three times as long as broad. Antennae a little shorter than body, first segment longer than the rest of the antennae, ratio of the antennal segments: 18:5:6:5, the last segment slightly flattened near apex. Pronotum transverse, anterior and posterior margins straight; mesonotum very large, moderately convex, a little widened posteriorly; metanotum about one half of the mesonotum in length, lateral portions much protruded anteriorly, divided into two portions by a distinct transverse ridge, the anterior portion about five times as long as the posterior one, with a conspicuous tubercle-like process in the middle of the ridge (well observable in profile). The characters of the legs are given in the generic description. Abdomen broad and short, about as long as mesonotum, narrowed posteriorly; first four segments nearly equal in length, fifth slightly shorter than the preceding three segments taken together, sixth a little shorter than the fifth. Connexivum broad, almost perpendicularly erect, forming a very conspicuous, long, stout spine-like process at the end, which is almost as long as the last two dorsal abdominal segments taken together, directed inwardly and crossed with each other at the apex. First four ventral abdominal segments very short, increasing the length from first to fourth; fifth much longer than fourth, nearly as long as third and fourth taken together; sixth very long, nearly as long as three preceding segments taken together, much rounded and narrowed posteriorly. Genital segments very small, mostly inserted in the sixth segment.

"Length of body 7 mm., breadth of body 2.3 mm., length of intermediate femur 9.5 mm., length of intermediate tibia 5.5 mm., length of posterior femur 8.5 mm., length of posterior tibia 3.5 mm.

"Male and macropterous forms are unknown.

"Habitat: Malay Peninsula."

The above original description and the figures given by Esaki require reinterpretations in certain respects. Esaki evidently believed that the metanotum is divided into two portions, *i. e.*, anterior and posterior portions as in his previous works on the Gerridae, but the posterior portion is actually the first abdominal tergite. Thus the italicized part in the above description should be read "anterior margin of first tergite distinct, metanotum much longer than first tergite." In his figure *a*, the metacetabular suture runs obliquely forward, instead of rearward, to reach the intersegmental suture between the mesonotum and metanotum. The direction of the suture is very probably wrong, the suture in all other genera of the subfamily runs obliquely caudad dorsally to reach the anterolateral angle of the first abdominal tergite. He says that the first tarsal segment of the hind leg is twice the length of the second segment.

If this is true this genus is quite unique in this character, since the first tarsal segment of the hind leg is always about as long as or even shorter than the second segment in all other genera of the Ptilomerinae.

SUBFAMILY HALOBATINAE BIANCHI

Halobatinae Bianchi, Ann. Mus. St. Petersbourg for 1896, p. 69(1896).
Halobatinae Bergroth, Ohio Nat., 8:371(1908).
Halobatinae Kenaga, Univ. Kansas Sci. Bull., 27(9);169-183(1941).
Halobatini Kirkaldy, Trans. Amer. Ent. Soc., 37:244, 249(1911).
Halobatitae Kirkaldy, Ann. Soc. Ent. Belg., 43:509(1899).
Halobatinaria Distant, Faun. Brit. Ind., Rhynch., 2:186(1903).

Structures in wingless forms: Body small, a little longer than wide. Head with anterior margin broadly rounded except for marine genera. Clypeus with basal margin obliterated except for marine genera. Eye with inner margin feebly rounded, covering posteriorly at least anterior half of pronotum. Antenniferous tubercles not or weakly developed except for marine genera. Antenna slender, shorter than length of body; first segment longest, shorter or longer than second and third segments together; *relative length of second to third segment greater in males than in females except for marine genera;* third segment modified in males of *Esakia;* fourth segment slender and simple in most genera, or short and more or less strongly curved in some genera. Mandibular and maxillary plates distinct from each other. Rostrum relatively short; third segment less than three times as long as last segment in great majority of species.

Pronotum not prolonged, much shorter than head in some genera. Intersegmental suture between mesonotum and metanotum dorsally represented by posterior margin of mesothoracic scutoscutellum, laterally obliterated except for *Asclepios.* Longitudinal suture separating mesopleuron from mesonotum absent in all genera. Mesosternum without paired longitudinal suture. Metanotum with median longitudinal sulcus indistinct or absent, metanotal lateral longitudinal suture rather weakly developed except for *Esakia.* Metacetabular suture dorsally approaching anterolateral angle of first tergite in some genera. Metathoracic spiracle small and longitudinally placed. Metasternum much reduced, represented by a short transverse subtriangular plate either reaching or not reaching metacetabula laterally or by omphalium alone; omphalium borne on apical margin of metasternum; omphalial groove absent. Front leg with femur and tibia have modification on inner margin in some genera; tarsus with first segment highly reduced except for *Halobates;* second segment much longer than first except for *Halobates;*

claws always arising preapically and with arolium. Middle leg always considerably longer than hind leg; femur considerably longer than tibia in most genera; tibia with a row of long hairs throughout inner margin in marine genera; first tarsal segment several times as long as second segment in most species, with a row of long hairs on inner margin in *Halobates.* Hind leg with coxa more or less prolonged in marine genera; tibia about half as long as or less than half as long as femur; first tarsal segment about as long as second segment in majority of species, first and second tarsal segments fused in *Halobates.*

Abdomen with ventrite more or less greatly reduced; first tergite with anterior margin distinct in most species, nearly straight; second and third tergites with their anterior margins, when distinct, roundly produced anteriorly. First ventrite absent. Connexivum with anterior segments often fused, not reflexed on dorsum, without connexival spine.

Male: Seventh segment longer than a preceding segment or segments ventrally, simply concave or nearly horizontal on ventral apical margin. Eighth segment more or less greatly prolonged, modified dorsally in *Halobates.* Ninth segment with suranal plate simple; pygophore with apical margin simply rounded except for *Eurymetropsis,* in which it is strongly bifurcate; rotated in some species of *Halobates;* parameres present except for marine genera, in which it is highly reduced or lost. Endosoma with definitive dorsal plate always curved back along apical margin of endosoma (fused part of apical plate); basal plate arising from behind base of dorsal plate or indistinguishably fused with dorsal plate; lateral plates always present, usually in basal half of endosoma; ventral plate slender and long, membranous apically.

Female: Seventh segment greatly prolonged, simply concave in ventral apical margin except for *Metrocoris,* in which ventral apical margin more or less greatly developed and modified in shape. First valvula either membranous or thinly sclerotized along outer margin; inner lobe small and fused with vulva except for *Esakia,* in which inner lobe is folded beneath outer lobe; outer lobe differentiated or split into hairy inner region and outer region in marine genera; ramus connected with process of ninth tergite on its outer margin. Second valvulae convergent apically; intervalvular membrane always with paired lateral membranous lobes which converge apically, a fine transverse dark stripe above apical margin of intervalvular membrane. Vulva simply rounded, membranous or thinly sclerotized along apical margin in most species.

TABLE 13.—Table of significant generic characters in Halobatinae.

	Asclepios	Halobates	Metrocoris	Eurymetra	Eurymetropsis	Eurymetropsiella	Eurymetropsielloides	Esakia	Ventidius (Ventidius)	Ventidius (Ventidioides)
4.......	(+)	(+)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
5.......	(+)	(+)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
9.......	(+)	(+)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
15B.....	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(—)	(—)	(—)
21A.....	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(+)	(+)
21B.....	(+)	(+)	(+)	(+)	(—)	(+)	(?)	(—)	(+)	(+)
22A.....	(+)	(+)	(—)	(—)	(?)	(?)	(?)	(—)	(—)	(—)
23.......	(+)	(+)	(+)	(+)	(—)	(±)	(±)	(+)	(+)	(+)
33.......	(+)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
35.......	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(±)	(±)
36.......	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(—)	(—)	(—)
40.......	(+)	(+)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
49.......	(+)	(—)	(+)	(+)	(—)	(+)	(+)	(±)	(±)	(—)
54, 56....	(+)	(±)$^{\times}$	(+)	(+)	(—)	(+)	(+)	(+)	(±)$^{\times}$	(—)
62A.....	(+)	(+)	(—)	(+)	(+?)	(+)	(?)	(+)	(+)	(+)
63B.....	(+)	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
68B.....	(+)	(—)	(+)	(+)	(+)	(+)	(—?)	(+)	(+)	(+)
69A.....	(±)	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
70.......	....	....	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(—)
72A.....	(+)	(±)$^{\times}$	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
74.......	(+)	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(+)	(+)
100.......	(+)	(+)	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(+)
101.......	(—)	(+)	(±)$^{\times}$	(+)	(—)	(—)	(+)	(+)	(+)	(—)

TABLE 13.—Table of significant generic characters in Halobatinae.—*Concluded*

	Asclepios	Halobates	Metrocoris	Eurymetra	Eurymetropsis	Eurymetropsiella	Eurymetropsielloides	Esakia	Ventidius (Ventidius)	Ventidius (Ventidioides)
102.......	(—)	(—)	(±)	(±)	(±)	(±)	(±)	(±)	(+)	(+)
103A.....	(+)	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(+)	(+)
107.......	(—)	(—)	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(+)
109.......	(+)	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
112.......	(—)	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
114.......	(+)	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
125.......	0.15–0.28:1	0.37–1.14:1	0.13–0.23:1	0.18–0.33:1	0.4:1	0.58:1	0.23:1	0.15:1	0.18–0.27:1	0.18:1
126.......	0.76–0.81:1	0.50–0.75:1	0.64–0.84:1	0.60–0.70:1	0.54:1	0.64:1	0.63:1	0.60–0.72:1	0.53–0.61:1	0.53:1
127.......	2.2–2.3:1	2.7–6.7:1	4.6–8.0:1	4.7–6.6:1	5.0:1	?	5.6:1	4.2–6.3:1	4.6–7.2:1	4.6:1
128.......	0.50–0.57:1	0.47–0.92:1	0.61–0.80:1	0.43–0.68:1	0.43:1	0.41:1	0.40:1	0.24–0.33:1	0.41–0.52:1	0.32:1
129.......	0.5–0.6:1	....	0.7–1.1:1	1.1–1.3:1	0.75:1	0.8:1	0.9:1	0.6–0.9:1	0.83–2.0:1	0.8:1
Total..	(+)23 (±) 1 (—) 4	(+)16 (±) 2 (—)10	(+)20 (±) 2 (—) 7	(+)21 (±) 1 (—) 7	(+)14 (+?)1 (±) 1 (—)12 (?) 1	(+)18 (±) 2 (—) 8 (?) 1	(+)17 (±) 2 (—) 6 (—?)1 (?) 3	(+)16 (±) 2 (—)11	(+)18 (±) 3 (—) 8	(+)16 (±) 1 (—)12

For the explanations of symbols see introduction and table 5.

Winged forms: Hemelytra with embolium always well formed along front margin of hemelytra. R + M + Cu branched into anterior R + M and posterior Cu. R + M either connected or not connected with embolium by oblique vein; Cu joined with A apically. Line of weakness absent.

Distribution: Oriental, Palaearctic and Ethiopian regions. The Pacific, Atlantic and Indian Oceans, Red sea.

Relationships of genera

The marine Halobatini, which includes two genera, *Asclepios* and *Halobates,* are quite distinct from the fresh water genera by some characters adaptive to the marine habitat and by peculiar modifications in the male apical abdominal segments, while retaining some characters more primitive than any fresh water genus. *Halobates* is nothing but a specialized group of *Asclepios.*

Among the fresh water genera, *Metrocoris* and *Eurymetra* have the highest number of primitive characters and they are closely related. While *Metrocoris* is confined to the Oriental region, *Eurymetra* occurs in Africa. In Africa there occur two other *Eurymetra*-like genera, *Eurymetropsis* and *Eurymetropsiella.* They have become distinct from *Eurymetra* by further specialization in certain structures as noted from table 13. The other rather remotely related genera, *Ventidius* and *Esakia,* occur solely in the Oriental region. They are different from the rest in the shorter pronotum, larger eyes, and the rather strongly flattened metacetabula, etc. *Ventidius (Ventidioides)* is nothing but a specialized group of *Ventidius s. str.,* but *Esakia* has become quite distinct from *Ventidius* with acquisition of some specialized characters, such as the strongly modified third antennal segment in the male, etc. *Eurymetropsielloides,* though occuring in Africa, shares some more or less important characters in common with the *Ventidius-Esakia* complex, such as the shorter pronotum and large eyes, but the narrow and simple metacetabulum is like that of *Metrocoris.*

The relationships of genera may be expressed as in diagram 8.

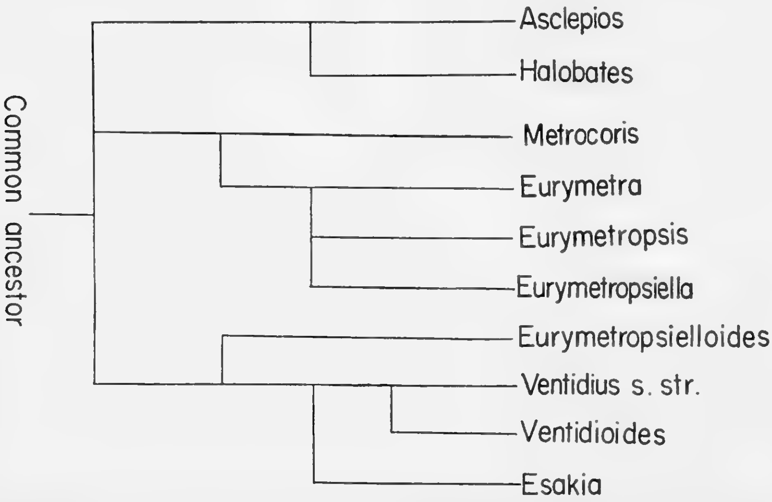

DIAGRAM 8—Diagram showing the relationships of genera of the Halobatinae.

Tribe HALOBATINI Bianchi

Color pattern: Predominately black dorsally, clothed with short velvety hairs. Head yellow to orange along eyes.

Structures in wingless forms: Head with anterior margin feebly produced medially and on each side of the middle; basal margin of clypeus distinct. Antenniferous tubercles produced forward. Intersegmental suture between mesonotum and metanotum absent dorsally in most species. Metasternum greatly reduced but reaching laterally metacetabular regions. Front leg has tibia without conspicuous inner apical process; first tarsal segment about as long as or a little shorter than second in most species. Middle leg with tibia provided with a row of hairs in all species; first tarsal segment with a row of hairs in most species. Hind leg with tarsal segments fused in *Halobates*; coxa longer than wide. Abdomen has the anterior margin of first tergite obliterated in most species. Male eighth segment with dorsal apical angle produced in most species; ventrolateral angle of male eighth segment with conspicuous process in all species. Ninth segment with suranal plate provided with more or less conspicuous projection at middle in most species; parameres highly reduced or absent.

Distribution: Temperate and tropical zones of the Pacific, the Indian, and the Atlantic oceans, and the Red sea.

Evolutionary tendencies peculiar to Halobatini

Both *Asclepios* and *Halobates,* while maintaining the same basic structural pattern as the fresh water genera of the same subfamily, exhibit some quite peculiar evolutionary trends as follows:

(1) The body surface is clothed with short velvety hairs.

(2) The wings are always absent.

(3) The body size has apparently become larger in the course of evolution.

(4) The first tarsal segment of the front leg has presumably become longer in the course of evolution.

(5) A row of long hairs on the middle tibia occur in both *Asclepios* and *Halobates,* the row of long hairs occurs also on the middle first tarsal segment in addition to the middle tibia in the specialized genus, *Halobates.*

(6) The hind coxa has apparently become prolonged.*

(7) The hind tarsal segments have become fused in the more specialized genus, *Halobates.**

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* Occurs also in other subfamilies.

(8) Modifications of the posterior ventrolateral and dorsolateral angles of the eighth segment in the male (process) have become more conspicuous in the more specialized genus, *Halobates.*

(9) The parameres have become vestigial or lost, while well retained in the fresh water genera.

(10) The suranal plate has become conspicuously widened at the middle in the more specialized genus, *Halobates.**

While some of the above-mentioned evolutionary tendencies are adaptive ones to the marine habitat, others appear to have nothing to do with the peculiar habitat (*e. g.*, modifications of the abdomen). In spite of the high degrees of specialization of the above mentioned structures, the tribe Halobatini has remained more primitive than the fresh water genera in the following structures:

(1) The basal margin of the clypeus is distinctly retained.

(2) The antenniferous tubercles are also retained and the anterior margin of the head in dorsal view is, therefore, not simply rounded as in the fresh water genera.

(3) The intersegmental suture between the mesonotum and metanotum is clearly retained laterally and is continuous to the metathoracic spiracle in *Asclepios* and some species of *Halobates.*

(4) The metasternum, though much reduced, reaches the metacetabular region laterally.

Modifications of the abdomen in Halobatini
(Figs. 751, 756, 770-776)

The male seventh segment: In *Asclepios* the seventh segment is prolonged but the ventral apical margin is concave, and the segment is transverse ventrally (fig. 751). In *Halobates* the segment is more prolonged and the ventral apical margin is nearly straight or even slightly produced medially. In *H. proavus, sericeus, japonicus, sobrinus,* and *hayanus* the seventh ventrite is twice as wide as long; in *H. mariannarum* (fig. 774) the seventh segment is less than twice as wide as long; in *H. splendens, flaviventris* and *micans* (fig. 770) the seventh ventrite is only slightly wider than long; in *H. hawaiiensis* (fig. 773) it is almost as long as wide.

The male eighth segment: In *Asclepios* (figs. 748, 751) the eighth segment is well exposed both dorsally and ventrally; the dorsal apical margin is simply rounded or feebly concave and the ventral processes are relatively short and simply rounded apically. In *Halobates* the eighth segment is more or less hidden beneath the more prolonged seventh segment. The dorsal lateral angle is pro-

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* Occurs also in other subfamilies.

vided with an obtuse process of varying degrees of development. The ventral paired lateral processes are simple but longer in *H. hayanus, sericeus, japonicus, sobrinus, flaviventris* and *proavus* than in *Asclepios;* they are thickened and truncate at apices in *hawaiiensis* (fig. 772); they are strongly asymmetrical in *mariannarum* (fig. 774) *splendens* and *micans.*

The male ninth segment: The suranal plate in *Asclepios* is simple although widened at middle. In *Halobates* the median widening is least conspicuous in *mariannarum;* more conspicuous and nearly rectangularly produced laterally at the middle in *germanus, japonicus, sericeus, splendens,* and *hayanus*; subrectangularly produced laterally and with a fine process at the middle of each side in *hawaiiensis* and *micans;* with a conspicuous process at the middle in *flaviventris* and *sobrinus.* The pygophore is not rotated in *Asclepios,* but it is rotated in *H. splendens* and *H. mariannarum* (fig. 774).

The female seventh segment: In *Asclepios* the seventh ventrite is broadly concave and relatively short. In some species of *Halobates* (*proavus, sericeus*) the seventh ventrite is relatively short and the ventral apical margin is somewhat concave, but in all others the seventh ventrite is more prolonged and the apical margin is nearly straight or even slightly produced at the middle; in *hawaiiensis* (fig. 771) the basal margin of the seventh ventrite is broadly concave and the apical margin is feebly bisinuate.

Modifications of the other structures in Halobatini

The body size: As already noted, *Asclepios* is more primitive in many characters than in *Halobates* but the size of the body (45-57)* is definitely smaller than *Halobates.*** In *Halobates,* as noted from the preceding discussion of the evolution of the abdomen, there is a rather striking tendency for the body size to be generally smaller in the species with more primitive abdomens, such as *proavus* (56), *sericeus* (54), *germanus* (58), *hayanus* (69), *sobrinus* (67), *japonicus* (69) than in the species with generally more specialized abdomens such as *mariannarum* (75), *hawaiiensis* (87), *splendens* (81). It appears that the prolongation of the seventh segment in both sexes is at least a great contributing factor toward the enlargement of the body in the larger species. The body size has apparently become larger in the evolution of these marine genera, contrary to the tendency toward reduction of the body size which prevails in the great majority of the groups of the Gerridae.

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* The numerical values represent values for the male body length.

** According to Dr. R. L. Usinger (in conversation) *Asclepios annandalei* Distant is quite large in size.

Genus *Asclepios* Distant

(Figs. 40, 138, 159, 748-759, 765-766)

Asclepios Distant, Ann. Mag. Nat. Hist., 15:504 (1915).
Asclepios Esaki, Ent. Month. Mag., 66:158-161 (1930).

Type species: *Asclepios annandalei* Distant, monobasic.

Species examined: *A. apicalis* Esaki, *A. coreanus* Esaki, *A. coreanus miyamotoi* Esaki.

Color pattern: Predominately grayish black above. Head orange yellow with a black spot on centre. Pronotum with posterior margin and on median longitudinal axis, meso- and metapleural regions orange yellow. Legs, antennae, and body beneath orange yellow to yellow.

Structures in wingless forms: Head between eyes wider at base than long at middle. Eye small, exserted, posteriorly covering anterolateral angle of pronotum. Antenniferous tubercles somewhat developed. Antenna has first segment longest, about as long as or a little longer than two following segments together, sparsely armed with small black bristles; second segment simply slightly thickened apically, apex truncate, a little longer than third segment; third segment simply slightly thickened anteriorly, apex truncate, also sparsely armed with short bristles; fourth segment about as long as or a little longer than third, fusiform. Rostrum short and robust, third segment a little less than twice as long as last segment.

Intersegmental suture between mesonotum and metanotum more or less distinct, traceable laterally as far as metathoracic spiracle, anteriorly produced obtuse angulately at middle. Mesonotum without distinct median longitudinal sulcus, simply convex; metacetabular suture almost reaching anterolateral angle of first tergite. Metasternum very short, about as long as second ventrite but extends laterally as far as inner margin of posteriorly produced metacetabula; omphalium vestigial, represented by a small tubercle on middle of posterior margin. Front leg has femur strongly thickened at base, then straightly narrowed apically in male and with many short and fine black spines on inner margin; tibia thickened on inner margin, inner apical process conspicuous; tarsus with first segment very short; second segment several times as long as first, claws arising from inner margin at basal third, with fine arolium. Middle leg with femur a little longer than tibia; tibia ciliated on almost entire inner margin, a little over twice as long as first tarsal segment; first tarsal segment slightly curved and thickened at base, a little over twice as long as second segment;

second segment with highly reduced claws. Hind leg shorter than middle leg, femur twice or a little less than twice as long as tibia; tibia eight to nine times as long as first tarsal segment or three to a little less than three times as long as first and second segments together; first tarsal segment much shorter than second segment; second segment with paired claws arising from basal region of inner margin, with fine arolium, fine hairs arising from apex and dorsal margin.

Abdomen strongly declivent. Anterior margin of first tergite distinctly retained, those of first and second produced anteriorly at middle. Ventrites greatly reduced in length.

Male: Seventh segment ventrally a little shorter than whole preceding abdominal segments together. Eighth segment cylindrically prolonged, ventrally with a pair of processes protruding posteriorly on each side. Ninth segment with suranal plate narrowed apically, dilated at middle, longitudinally elevated on dorsal surface along median longitudinal axis; pygophore with apical margin rounded; parameres vestigial. Endosoma with definitive dorsal plate extending along apical margin of endosoma, robust and bifurcate apically, basally extending along basal margin of endosoma; ventral plate slender, rising from upper part of basal margin of endosoma, reaching apical margin of endosoma; paired lateral plates long; a slender U-shaped sclerite extends over dorsal plate from both sides. (Description of the genitalia is based on *coreanus.*)

Female: Seventh segment a little longer than second to sixth segments together ventrally, apical margin broadly concave. Eighth segment well developed ventrally. First valvula with inner lobe short and fused with membranous vulva; outer lobe with oblique rows of hairs on almost entire surface of inner half, apical region of the lobe membranous, acute at tip; ramus arising from near apex of outer lobe; apex of process of ninth tergite with crescent shaped plate. Second valvula with two apical lobes, outer one more conspicuous, inner lobe hook-shaped, directed caudally at apex. (Description of the genitalia is based on *coreanus miyamotoi.*)

Distribution: Off or along the coasts of India, Formosa, Japan, Korea.

The genus *Asclepios* is more primitive than *Halobates* in the following characters:

(1) The intersegmental suture between the mesonotum and the metanotum is always distinct and traceable laterally as far as the metathoracic spiracle.

(2) The first and second tarsal segments of the hind leg are distinct from one another.

(3) The row of long hairs on the middle leg is confined to the tibia.

(4) The anterior margins of the basal abdominal tergites are distinct.

(5) The suranal plate is less strongly widened posteriorly.

(6) The male genitalia have the parameres retained and the eighth abdominal segment of the male much less modified.

Genus *Halobates* Eschscholtz

(Figs. 41, 138, 159, 760-766, 767-776)

Halobates Eschscholtz, Entomographien, p. 102(1822).
Halobates Laporte, Essai Classif. Hem., p. 24(1833).
Halobates Mayr, Reise Freg. Novara, Zool. II, Hem., pp. 169 and 177(1868).
Halobates Buchanan-White, Challenger Rep. Zool. VII, 19:23(1883).
Halobates Distant, Faun. Brit. Ind. Rhynch., 2:186(1903).
Halobates Kirkaldy, Trans. Amer. Ent. Soc., 32:156(1906).
Halobates Oshanin, Verz. Palaearkt. Hemip., 1:500(1908).
Halobates Distant, Faun. Brit. Ind., Rhynch., 5:152(1910).
Halobates Van Duzee, Cat. Hem., p. 431(1917).
Halobates Hungerford, Univ. Kansas Sci. Bull., 21:116, 120(1919).
Halobates Torre-Bueno, Connecticut Geol. and Nat. Hist. Survey Bull. 34:662 (1923).
Halobates Esaki, Ann. Mus. Nat. Hung., 23:130(1926).
Halobates Esaki, Dobutsugakuzasshi, 41(491):382-384(1929).
Halobates Esaki, Botany and Zoology, 1:771-784(1933).
Halobates Usinger, Proc. Haw. Ent. Soc., 10(1):77-84(1938).

Type species: *Halobates micans* Eschscholtz, by subsequent designation (Laporte, 1833 in the above reference).

Species examined: *H. flaviventris* Eschscholtz, *H. germanus* B.-White, *H. hayanus* B.-White, *H. hawaiiensis* Usinger, *H. japonicus* Esaki, *H. mariannarum* Esaki, *H. micans* Eschscholtz, *H. proavus* B.-White, *H. sericeus* Eschscholtz, *H. sobrinus* B.-White, *H. splendens* Witlaczil.

Color pattern: Black in ground color, gray pubescent throughout almost entire body in varying densities in various species. Head always with a pair of orange yellow spots, which are often confluent. Body beneath concolorous with body above.

Structures in wingless forms: Head wider at base than long in middle. Eye small, covering anterolateral angle of pronotum. Antenniferous tubercles somewhat developed. Antenna with first segment considerably longer than second and third segments together in most species, thickened and truncate at apex; second segment about as long as or more often longer than third segment, apex truncate; fourth segment fusiform, always longer than third segment. Rostrum short and robust, third segment less than twice as long as last segment.

Intersegmental suture between mesonotum and metanotum normally lost though present in nymphs, occasionally recognizable as a faint suture in adults. Metanotum without distinct median longitudinal sulcus; metacetabular suture dorsally approximated to anterolateral angle of first abdominal tergite. Metasternum very short, but reaching laterally to inner basal angle of posteriorly produced metacetabular; omphalium vestigial, represented by a small tubercle at middle of posterior margin of metasternum. Front leg with femur sparsely armed with long fine hairs on inner margin, with some stiff, black bristles on inner margin at base, thicker and flattened at base in males of some species; tibia thickened apically on inner margin, process at inner apical angle conspicuous; tarsus relatively long, first segment shorter than second segment in most species, but at least one third as long as the latter, second segment with claws arising from inner margin before middle, claws with fine arolium. Middle femur one and one third to a little over twice as long as tibia; tibia ciliated on inner margin, usually less than twice as long as first tarsal segment; second segment with apex clothed with short hairs, straight long hairs arising from dorsal margin near apex, highly reduced fine claws arising from near apex. Hind leg shorter than middle leg; femur about twice as long as tibia except for *splendens* and *micans*, in which femur a little longer than tibia; tibia about three to a little less than four times as long as tarsus; tarsus with first and second segments completely fused, claws arising from beyond middle, with fine arolium, apex with a short hair, and a long hair arising from upper margin near apex.

Abdomen strongly declivent. Anterior margins of basal abdominal tergites at least medially obliterated normally, those of first and second produced anteriorly when traceable. Ventrites strongly reduced in lengths.

Male: Seventh segment strongly developed ventrally, longer than all preceding segments together in some species, as long as or a little shorter than sixth segment dorsally. Eighth segment with dorsal apical margin roundly produced, with a pair of lateral processes of various shapes in some species, ventrally with a pair of slender lateral processes, their apices vary in shape in various species, asymmetrical in some species. Ninth segment with suranal plate provided with a more or less conspicuous projection at middle of each side in most species; pygophore more or less rotated in some species; parameres absent. Endosoma with definitive dorsal plate strongly thickened, turned back and bifurcate at apex, represented by two slender plates medially, reaching basal margin of endosoma; ventral plate indistinguishably fused with dorsal plate, broad and thin, apically membranous, circled dorsocephalad; long, U-shaped slender plate not stretching over dorsal plate; lateral plates rather short and robust, placed in basal half of endosoma. (Description of the genitalia is based on *H. sobrinus*).

Female: Seventh segment well developed ventrally, longer than all preceding ventrites together in some species, transverse and trapezoidal in shape in most species, simply concave or bisinuate on ventral apical margin. Eighth segment exposed both dorsally and ventrally. First valvula split into inner hairy region and outer shorter region, both simply narrowed apically, their apices subacute, inner lobe fused with vulva; process of ninth tergite, to which ramus of first valvula is attached, is lacking crescent shaped plate at apex. Second valvulae convergent apically, acute at tips; intervalvular membrane on apical margin bilobed and each lobe acutely pointed. (Description of the genitalia is based on *H. sobrinus.*)

Distribution: Temperate and tropical zones of the Pacific, Indian, and Atlantic oceans and the Red sea. Eskai (1933) listed two species of *Halobates* (*H. micans* and *H. inermis*) as occurring in the Atlantic ocean.

Tribe METROCORINI Matsuda

Color pattern: Uppersurface of body mottled with yellow and black stripes, bands, or spots.

Structures in wingless forms: Head with anterior margin broadly rounded. Clypeus with basal margin obscure or lost. Antenniferous tubercles scarcely developed.

Intersegmental suture between mesonotum and metanotum distinct dorsally in most species, lost laterally in all species. Metasternum laterally not reaching metacetabular regions. Front leg has inner apical process of tibia conspicuous; first tarsal segment always short, much shorter than second segment in most species. Middle tibia without conspicuous row of hairs in most genera. Hind tarsal segments always distinct from one another; coxa about as long as wide.

Abdomen with anterior margin of first tergite distinct in most species. Male eighth segment prolonged in some species, without conspicuous modification. Male ninth segment with suranal plate simple; parameres always present.

Distribution: Temperate and tropical zones of the Eastern Hemisphere.

Genus *Metrocoris* Mayr

(Figs. 45, 108, 121, 139, 158, 167, 777-796)

Metrocoris Mayr, Verh. Zool. Bot. Gesell., Wien. 15:455(1865).
Metrocoris Mayr, Reise Freg. Novara, Zool., Hem., 2:178(1868).
Metrocoris Meinert, Ent. Medd., 1:140(1888).
Metrocoris Distant, Faun. Brit. Ind., Rhynch., 2:188(1904).
Metrocoris Kirkaldy, Entomologist, 37:61(1904).
Metrocoris Distant, Faun. Brit. Ind., Rhynch., 5:158(1910).
Metrocoris Esaki, Ann. Mus. Nat. Hung., 23:122-130(1926).
Metrocoris Esaki, Ann. Mag. Nat. Hist., 10(2):511-512(1928).
Metrocoris Esaki, Ann. Mag. Nat. Hist., 10(4):417-418(1929).
Metrocoris Lundblad, Arch. Hydrobiol. Suppl. 12, Tropische Binnengewässer, 4:394-399(1933).
Halobatodes B.-White, Challenger Rep. Zool., 7(13):23, 58(1883) (type species, *Halobatodes histrio* Buchanan White).
Gerastratus Distant, Ann. Mag. Nat. Hist., 8(5):148(1910) (type species, *Gerastratus foveatus* Distant).
Euodes Distant, Faun. Brit. Ind., Rhynch., 5:162(1910) (type species, *Euodes communis* Distant).
Metrocoropsis Paiva, Rec. Ind. Mus., 16:365(1919) (type species, *Metrocoropsis femorata* Paiva).

Type species: *Metrocoris brevis* Mayr, monobasic.

Species examined: *M. histrio* (B.-White), *M. lituratus* (Stål), *M. squamifer* Lundblade, *M. ståli* (Dohrn)(?), *M. strangulator* Breddin, *M. nigrofasciatus* Distant, and two unidentified species.

Color pattern: Pale yellow in ground color. Head usually with a median large black marking. Pronotum in wingless forms with a single median and a pair of lateral longitudinal black stripes which are confluent anteriorly. Mesonotum with a single median and two pairs of lateral black stripes, the outer pair often confluent with transverse black stripe on intersegmental suture; black along anterior margin of mesonotum. Metanotum with median longitudinal and a pair of lateral oblique black stripes which meet laterally with the stripes from the intersegmental suture and the stripe coming from metathoracic spiracle; black transverse stripe along metacetabular suture and metacetabula has a black longitudinal stripe. Abdomen largely black on upper surface, pale yellow to yellow on undersurface. Pronotum in winged form always with median longitudinal black stripes reaching near apex, with a pair of lateral black stripes in posterior lobe, black along anterior margin of pronotum. Hemelytra nearly black, with darker veins.

Structures in wingless forms: Male larger than female in some species. Head including eyes usually over twice as wide as long in the middle. Eye exserted, covering most part of anterolateral angle of pronotum. Antenna relatively longer in male than in female; first segment much longer in male than in female, longest in both sexes, often longer than second and third segments together, third segment with inconspicuous basal peduncle, both second and third segments gradually thickened anteriorly and subtruncate at apices, relative length of second to third greater in male than in female; fourth segment shortest. Rostrum slightly extending beyond posterior margin of prosternum; third segment about three times as long as last segment.

Pronotum shorter than head at middle, lateral margin rounded, posterior margin concave. Intersegmental suture between mesonotum and metanotum more or less concave dorsally, obliterated laterally. Metanotum without median longitudinal sulcus; metacetabular suture distinct, reaching dorsally anterolateral angle of first tergite; metacetabulum narrow, posterior margin simply oblique, posterolateral angle not flattened; metanotal lateral longitudinal suture weakly developed, not reaching intersegmental suture. Metasternum highly reduced, represented by small transverse subtriangular plate bearing omphalium at middle of posterior margin. Front leg with femur lacks tubercle, occasionally thickened and with conspicuous processes on inner margin in male (*strangulator*); tibia strongly thickened apically, with conspicuous inner apical angle which is defined by oblique depression on inner and outer surfaces, lacks a row of denticles on inner margin; tarsus with first segment very short, second segment long, claws arising from middle or beyond middle of the segment, and with membranous arolium. Middle leg with femur thickest, about one and one fifth to one and a half times as long as tibia; tibia gradually tapering apically, twice to a little over twice as long as first tarsal segment; first tarsal segment four and two thirds to six and a half times as long as second segment, second tarsal segment with claws arising preapically and with fine arolium. Hind leg with femur one and one fourth to a little over one and a half times as long as tibia; tibia about ten times as long as first tarsal segment; first tarsal segment about as long as second or shorter than second in some species, claws arising preapically.

Abdomen with anterior margin of first tergite bisinuate or sometimes obliterated; second tergite strongly angularly produced on anterior margin, to a lesser extent so is third tergite; fourth to seventh tergites subequal in length to each other. Connexivum reflexed. Ventrites much more strongly reduced than tergites. Abdominal spiracles, when recognized, placed closer to posterior margin than to anterior margin except for those of sixth ventrite which are at middle, those of seventh closer to anterior margin than to posterior margin.

Male: Seventh segment ventrally much longer than sixth segment, broadly concave on ventral apical margin. Eighth segment broadly rounded on apical margin dorsally, broadly concave on apical margin ventrally. Ninth segment with suranal plate usually hidden beneath well developed eighth tergite, simple, ventral basal angle with a foot shaped process on each side; pygophore broadly rounded on apical margin or rarely broadly dilated in apical half; parameres well developed and conspicuous. Endosoma with definitive dorsal plate turned cephalad on apical margin of endosoma, represented by two slender sclerites along dorsal margin; indistinguishably fused with ventral plate; ventral plate tapering apically and membranous, curved upward anterior to apical margin of endosoma; lateral plates two paired, upper one not well sclerotized. (Description of the genitalia is based on *ståli*(?).)

Female: Seventh segment ventrally strongly developed and modified in various shapes apically in various species (figs. 787, 788, 790), completely enclosing eighth segment above. First valvula with inner lobe short, more strongly sclerotized and fused to membranous vulva; outer lobe long and membranous, with acute tip; ramus extending on outer margin as far as apical third of the outer lobe and basally on outer margin of process of ninth tergite. Second valvula apically bilobed, outer one more robust, basally free from inner lobe, which is directly continuous with concave apical margin of intervalvular membrane; ramus fine. Vulva membranous, with short median projection. (Description of the genitalia is based on *ståli*(?).)

Winged forms: Pronotum subpentagonal in shape, with subhorizontal anterior margin and acute tip. Hemelytra with well developed embolium. R + M + Cu branches into two veins at basal third of the wing (R + M and Cu); two apical cells are formed beyond middle of wing. Vein A joins apically with apical end of lower one of the closed cells, also connected with rear margin of wing at middle by a short cross vein.

Distribution: The palaearctic and Oriental regions (Annam, Arabia, Burma, Ceylon, China, Formosa, India, Japan, Korea, Malaya, Nepal, Persia).

Genus *Eurymetra* Esaki

(Figs. 47, 797-807)

Eurymetra Esaki, Ann. Mus. Nat. Hung., 23:129(1926) (as subgenus of *Metrocoris*).
Eurymetra Esaki, Ann. Mag. Nat. Hist., 10(2):512(1928) (as genus).

Type species: *Metrocoris natalensis* Distant, by original designation.

Species examined: *E. natalensis* (Distant), *E. nitidulus* (Esaki), *E. angolensis* Hoberlandt, and one unidentified species.

Color pattern: Essentially as in *Metrocoris,* more lustrous in most species.

Structures in wingless forms: Head including eyes over twice as wide as long. Eye strongly exserted, covering most part of anterolateral margin of pronotum, anterior half of inner margin slightly rounded. Antenna relatively longer in male than in female; first segment relatively longer in male than in female, slightly curved and longest, usually about twice as long as second, truncate at apex; second segment nearly as long as or shorter than third; third segment with small simple peduncle; fourth segment fusiform, always shortest. Rostrum has third segment a little less than four times as long as last segment.

Pronotum short, lateral margins rounded and divergent posteriorly, posterior margin sinuate. Intersegmental suture between mesonotum and metanotum slightly concave at middle dorsally, directed obliquely forward laterally, lost in front of metathoracic spiracle. Metanotum without median longitudinal sulcus; lateral longitudinal suture weakly developed. Metacetabulum relatively wide, dorsal apical margin simply concave. Metasternum represented by a small transverse, subtriangular plate; omphalium distinct. Front leg with trochanter lacks tubercle; femur simple, slender, slightly curved and narrowed apically, with long hairs on inner margin at basal half, without tubercles on inner margin; tibia thickened apically, with rather conspicuous process at inner apical angle, which is defined by an oblique depression both on outer and inner surfaces, lacks denticles on inner margin; tarsus with first segment short; second segment three to five times as long as first segment, claws arising from near middle of lower margin of second segment and with membranous arolium. Middle leg with femur gradually tapering apically, one and a half to two and a third times as long as tibia; tibia two and two thirds to three and one third times as long as first tarsal segment; first tarsal segment a little over four to six and a half times as long as second segment, claws arising preapically and with arolium. Hind leg with femur over twice to about one and a half times as long as tibia; tibia eight to ten times as long as first tarsal segment; first tarsal segment a little longer than second segment, claws arising preapically.

Abdomen wider than in *Metrocoris.* First tergite with bisinuate anterior margin; second tergite with anterior margin strongly produced anteriorly, to a lesser degree so is anterior margin of third tergite; fourth to sixth tergites subequal in length. Connexivum more or less strongly reflexed. Abdominal spiracles of sixth and seventh segments located at middle between anterior and posterior margins.

Male: Seventh segment ventrally twice as long as sixth segment or about as long as second to sixth segments together (*nitidulus*), concave on ventral apical margin. Eighth segment well developed dorsally, covering suranal plate. Ninth segment with suranal plate subcylindrical, with a conspicuous pair of foot-shaped processes at outer basal angles; pygophore rounded on apical margin; parameres well developed. Endsoma with dorsal plate robust and turned cephalad apically, loosely connected with basal plate at dorsal basal angle of endosoma, slender looped sclerite stretches along and above dorsal plate; ventral plate indistinguishably fused to dorsal plate, slender and sclerotized except for apex which is membranous; lateral plates composed of two pairs, upper one of them stretch over the entire length of endosoma. (Description of the genitalia is based on *natalensis.*)

Female: Seventh segment well developed but not covering eighth segment ventrally. Eighth segment with first valvula sclerotized on outer margin, the rest membranous and with acute tip, inner lobe fused with vulva. Second valvula sclerotized along outer margin, apices convergent; intervalvular membrane with a pair of membranous processes converging apically. Vulva rounded on apical margin and with a median longitudinal ridge. (Description of the genitalia is based on *natalensis.*)

Winged forms: Not available for study.

Distribution: The Ethiopian region (Angola, Cameroons, Ethiopia, Ivory coast, Madagascar, Natal, Nigeria, South Africa).

The genus is closely related to *Metrocoris*, but can be distinguished by the union of the following characteristics:

(1) The body, especially the abdomen, is strongly widened at least in some species.

(2) The male genital segment is not prolonged as in *Metrocoris*.

(3) The uppersurface of the body lustrous.

(4) The seventh segment ventrally does not extend beyond the eighth segment in the female.

Genus *Eurymetropsiella* Poisson

(Figs. 48, 808-816, 818)

Eurymetropsiella Poisson, Rev. Zool. Bot. Afr. 33(1-2):73-76(1950).

Type species of the genus: *Eurymetropsiella schoutedeni* Poisson, by original designation.

Species examined: *E. schoutedeni* Poisson.

Color pattern: Predominantly black. Dark yellow spots on anterior and basal regions of head. Pronotum dark yellow on margin. Mesothorax and metathorax with several pairs of yellow spots as shown in figure 48. Legs nearly black. Body beneath largely pale yellow.

Structures in wingless forms: Body nearly globular and flattened. Mesonotum and metanotum greatly widened. Head including eyes over twice as wide as long. Eye covering anterolateral margin of pronotum, posterior end nearly reaching posterolateral angle of pronotum. Antenna thicker in male; first segment much longer than second, but shorter than second and third together; third segment shorter than second but longer than fourth, basal peduncle simple. Rostrum short and thick, extending beyond prosternum, third segment about twice as long as fourth segment.

Pronotum shorter than head, posterolateral angle rounded, posterior margin nearly straight. Mesothorax with humeral area slightly produced on either side of pronotum, widened posteriorly on either side of metacetabular region. Intersegmental suture between mesonotum and metanotum nearly straight and distinct only dorsally. Metanotum without median longitudinal sulcus; metanotal lateral suture absent; metacetabular suture absent. Metacetabula narrow, posterolateral angle not produced. Metasternum represented by small omphalium only, transverse subtriangular metasternal plate lost. Front leg sexually dimorphic, a mass of shaggy hairs on trochanter and femur occur only in male. Femur distinctly longer than tibia and slender; tibia with inner apical process separated by a longitudinal groove, acute at tip, bearing long curled hairs; tarsus a little shorter than tibia, first segment a little over half as long as second, claws arising from apical one third of second segment. Middle leg with femur thicker at base, about one and a half times as long as tibia; tibia curved, with two rows of hairs on inner margin throughout, a little less than twice as long as tarsus. Hind leg with coxa a little longer than wide; trochanter densely haired, femur about two and a half times as long as tibia; first tarsal segment a little shorter than second, second segment in lateral view much finer in apical half, claws not recognized in the specimen examined.

Abdomen in female: Dorsally strongly declivent. Anterior margin of first tergite distinct, broadly roundly produced at middle; anterior margins of second and third tergites also produced anteriorly; from sixth tergite on completely folded beneath fifth. First three connexival segments completely fused. Second to fifth ventrites greatly reduced, sixth ventrite as long as four preceding segments together.

Male: Parameres well developed. Pygophore narrowly rounded on apical margin (based on Poisson's figures and description, 1950).

Winged forms: Unknown.

Distribution: The Ethiopian region (Belgian Congo, French Congo, Togo).

The genus *Eurymetropsiella* is more specialized than *Eurymetra* in the following points:

(1) The antennae are sexually dimorphic.

(2) The second to fifth ventrites are more reduced.

(3) The metasternum is represented by the omphalium alone.

(4) The first three connexival segments are completely fused.

(5) The seventh abdominal segment of the female is ventrally greatly prolonged and apically infolded within the abdominal cavity.

The genus can be separated from *Eurymetropsis* Poisson by the following characteristics:

(1) The pygophore is simply rounded on the apical margin, while it is deeply notched on the apical margin in *Eurymetropsis.*

(2) The body is much wider.

(3) The intersegmental suture between the mesonotum and metanotum nearly straight dorsally.

(4) The metasternum is represented by the omphalium alone.

(5) The relatively long first tarsal segment of the front leg.

Genus *Eurymetropsielloides* Poisson

(Fig. 49, 845-853)

Eurymetropsielloides Poisson, Mem. Inst. Sci. Madagascar, Ser.E, 7:246-249 (1956)

Type species: *Eurymetropsielloides milloti* Poisson, monobasic. Since this genus was described for only a single species represented by a single male specimen which was not available for study, it has not been possible to redescribe it. The followings are the original description by Poisson and the additional remarks based on the drawings given by Poisson with his original description. The figures are copied from his work.

Original description: "*Eurymetropsielloides Milloti* n. g., n. sp.

"Cet Halobatinae est à rapprocher des genres *Eurymetropsis* Poiss. (Type *E. Carayoni* Poiss. du Cameroun), et *Eurymetropsiella* Poiss. (Type *E. Schoutedeni,* espèce africaine de l'Ituri à laquelle s'ajoute *E. congoensis* Poisson (1955), du Congo.

"Pigmentation générale noir sépia; une bande juanâtre au bord postérieur du vertex; deux tâches triangulaires de même teinte contre le bord postérieur du pronotum. Une bande jaune-flave de part et d'autre sur les côtés du thorax simulant un oiseau les ailes étendues vu postérieurement. Deux bandes jaunâtres, étroites, mésonotales, postérieures, précédées de deux petites taches presque rondes et plus centrales sur le disque du mésonotum. Une tâche médiane ovalaire transversalement sur le septième tergite, accompagnée d'autres tâches sur les hanches distribuées comme l'indique la figure (fig. 49 in this work). Une fine et courte pilosité cuivrée tapisse les tergites abdominaux II à V.

"Antennes noires; le 1 article jaunâtre à la base, le 4 article légèrement contourné en S:

55-35-(3)-31-(1.5)-21

Pattes antérieures noires, sauf la base du fémur jaunâtre; fémur armé de trois longues soies raides, implantées ventralement vers la base de L'article. Tibia non denté, seulement revêtu sur son bord ventral d'une courte et dense pilosité et prolongé par un éperon prétarsien, terminé par une courte brosse:

F.	T.	t
70	57	6 + 26

"Pattes intermédiaires: les plus longues; 1er article tarsien quelque peu renfle à son extremité antérieure et finement poilu en dessous:

F.	T.	t.
98	62	22.5 + 4

"Pattes postérieures

F.	T.	t.
101	41	8 + 9

"8^e segment abdominal cylindrique, mais quelque peu renflé vers l'avant (fig. 7, A). Capsule génitale peu acuminée et non bifurquée. Parameres symétriques, incurvés et spatulés.

"Longueur: 3.5 mm; largeur au niveau du mésothorax: 2.2 mm.

"Distrib.—1 mâle aptère, Sandrangato, Moramanga (Madagascar) (J. Millot, 1954).

"Obs.—Le genre *Eurymetropsielloides* n. g. diffère d'*Eurymetropsis* par la capsule génitale du mâle non bifurquée à l'extrémité, les tibias antérieures non armés de denticules, l'aspect général plus massif; il diffère d'*Eurymetropsiella* par ses pattes antérieures proportionellement plus courtes, aux articles plus épais, les tibias non finement dentés, seulement pourvus de courts poils densés; les fémurs non armés d'un denticule pileux; la capsules génitale moins conique; les paramères non aciculés; le vertex proportionellement plus large; les yeux débordant assez largement les côtes du pronotum.

"La tête est un peu plus large entre les yeux qu'elle n'est longue vue dorsalement; avec les yeux, elle est trois fois au moins plus large que longue. Corps : 1.5 fois a 1.6 fois plus long que large."

Remarks: The genus *Eurymetropsielloides* appears to be more closely related to *Ventidius* than to *Eurymetropsis* or *Eurymetropsiella* with which Poisson has compared it. The similarities to *Ventidius* are indicated in the following characters:

(1) The broad head between eyes. In the related genera of Poisson, the head between eyes is relatively narrow as in *Eurymetra* or *Metrocoris*, but in *Ventidius* and *Esakia* the head between eyes is broad as in *Eurymetropsielloides.*

(2) The eyes are elongate. In *Eurymetra* and related genera described by Poisson from Africa, the eyes are much shorter and more rounded on the anterior margin, not as much exserted as shown in figure 4 for *Eurymetropsielloides milloti,* while in *Ventidius* and *Esakia* the eyes are more elongate and completely cover the lateral margins of the pronotum, much as in *Eurymetropsielloides.*

(3) The pronotum is short as in *Ventidius* or *Esakia,* not as long as in the other genera occurring in Africa.

(4) The proportional lengths of antennal segments and leg segments are much as in a typical species of *Ventidius.*

This genus, however, differs from *Ventidius* by the metacetabula which are not flattened posterolaterally and by the different color pattern. Poisson apparently missed one abdominal segment (tergite) in his figure.

All abdominal tergites are clearly distinct from each other in his figure but the number of tergites is one less than it should be. The intersegmental suture between the mesonotum and metanotum is indicated only laterally in his figure.

Genus *Eurymetropsis* Poisson

(Figs. 46, 872-880)

Eurymetropsis Poisson, Rev. France. Ent., 15(3):169-171(1948).

Type species: *Eurymetropsis carayoni* Poisson, by original designation.

Species examined: *E. carayoni* Poisson.

Color pattern: Predominantly black. Head black except along dorsal basal margin of head and behind clypeus yellow. Antenna black. Pronotum along basal and lateral margins yellow. Mesonotum with a yellow longitudinal stripe extending back above mesocoxa; a pair of small yellow spots above intersegmental suture between mesonotum and metanotum, another pair of small yellow spots inside mesopleural yellow longitudinal stripe. Metanotum with two paired yellow spots in front of first tergite and metacetabular suture, and one spot of the same color on metacetabula. Legs black except bases yellow. Body beneath pale yellow.

Structures in wingless forms: Relatively elongate in body shape. Head including eyes much over twice as wide as eyes. Eye covering anterior half of lateral margin of pronotum. Antenna a little shorter than body; first segment longest, shorter than second and third segments together, dilated at basal third; second segment longer than third; third segment with a ear-shaped basal peduncle; fourth segment shortest and curved. Rostrum with third segment about two and a half times as long as last segment.

Pronotum relatively long, posterior margin slightly produced anteriorly at middle, lateral margin rounded, a little narrower than head including eyes. Mesonotum slightly widened posteriorly. Intersegmental suture between mesonotum and metanotum produced anteriorly at middle, obliterated laterally. Metanotum with a faint median longitudinal sulcus anteriorly, lacks metanotal lateral longitudinal elevation; metacetabular suture not reaching anterolateral angle of first tergite; metacetabulum relatively narrow, dorsal posterior margin simple and oblique, posterolateral angle not rounded. Male front leg with coxa lacks tubercle; femur provided with a small dark tubercle on inner margin at middle, sparsely clothed with long hairs on inner margin of trochanter and femur; tibia with a rather conspicuous process at inner apical angle, inner margin with a series of small black tubercles along inner margin; tarsus with first segment greatly reduced, second segment slender and long, claws arising from a little beyond middle of inner margin of second segment and with arolium. Middle leg with femur a little less than twice as long as tibia; tibia about twice as long as tarsus; tarsus with first segment five times as long as second segment. Hind leg with femur a little over twice as long as tibia; tibia about eight times as long as first tarsal segment; tarsus with first segment a little shorter than second segment.

Abdomen with anterior margin of first tergite obliterated, much longer than second tergite; basal abdominal tergites densely clothed with adpressed hairs and segmentations obscured; fifth to seventh tergites highly reduced in length. Ventrites also greatly reduced; seventh ventrite a little longer than the preceding.

Male: Eighth segment with a paired needle shaped processes (?), greatly prolonged. Ninth segment with pygophore strongly bifurcate apically. Parameres symmetrical and conspicuous. (Description is based on Poisson's figures on *carayoni* (1948.)

Winged forms: Unknown.

Distribution: The Ethiopian region (Cameroons).

Poisson says "8 segment abdominal du mâle présentent postérieurement des prolongement aciculés (fig 2, C)," but his figure 3A and B, (figs. 878, 879 in this work) which actually show the dorsal and ventral sides of the eighth segment, show no such modified structure. Figure 2, C (fig. 880) which Poisson thought to represent the eighth segment appears to be actually the suranal plate, and the spinous structures are probably the basal lateral foot-shaped processes of the suranal plate which frequently occur in the Gerridae. Unfortunately, the eighth and ninth segments are detached from the specimens which Dr. Poisson kindly lent for study, and are therefore not available for study to make this interpretation certain.

The genus *Eurymetropsis* can be differentiated from *Eurymetropsiella* by the following characteristics:

(1) The pygophore is strongly bifurcate on the apical margin.

(2) The anterior margin of the first abdominal tergite is obliterated.

(3) The intersegmental suture between the mesonotum and the metanotum is produced anteriorly at the middle.

(4) The body is more slender.

Genus *Ventidius* Distant

(Figs. 42-43, 122, 140, 160, 819-844)

Ventidius Distant, Ann. Mag. Nat. Hist., 8(4):150(1910).
Ventidius Distant, Faun. Brit. Ind. Rhynch., 5:157(1910).
Ventidius Paiva, Rec. Ind. Mus., 14:25(1917).
Ventidius Esaki, Jour. Fed. Malay Mus., 16:18(1930).
Ventidius Lundblad, Arch. Hydrobiol. Suppl. 12, Tropische Binnengewässer, 4:399(1933).
Ventidius Hungerford and Matsuda, Univ. Kansas Sci. Bull., 40(7):323-343 (1960)

Type species: *Ventidius aquarius* Distant, monobasic.

Species examined: *V. chinai* Hungerford and Matsuda, *V. distanti* Paiva ?, *V. henryi* Esaki, *V. kuiterti* Hungerford and Matsuda, *V. malayensis* Hungerford and Matsuda, *V. usingeri* Hungerford and Matsuda, *V. werneri* Hungerford and Matsuda.

Color pattern: Head including eyes over twice as wide as long in middle. Eye elongate, exserted, covering lateral margin of pronotum and anterolateral angles of mesonotum. Antenna slender and long, longer in male than in female. First segment always longest, sparsely armed with black bristles, with a tuft of hairs at distal end in *malayensis;* apex truncate; second segment has its relative length to third greater in male than in female; third segment shorter than second segment in larger species, or a little longer than second in smaller species, with a small basal peduncle; fourth segment longer than third (*malayensis*) subequal to or a little shorter than third. Rostrum short, third segment twice to a little over three times as long as last segment.

Pronotum short and transverse, both anterior and posterior margins concave, lateral margins rounded. Intersegmental suture indistinct though traceable dorsally in most species, the suture laterally obliterated in front of metathoracic spiracle in all species. *Mesosternum with a small black tubercle on median longitudinal axis in kuiterti,* Metanotum without median longitudinal sulcus; lateral longitudinal suture not reaching intersegmental suture; metacetabular suture reaching dorsally anterolateral angle of first abdominal tergite; metacetabulum relatively broad, posterolateral angle more or less flattened and somewhat produced. Metasternum represented by a small transverse subtriangular plate bearing omphalium on it. Front leg relatively long and slender; trochanter lacks tubercle; femur with a small tubercle on inner margin of male in *kuiterti*, slender and simple in other species, sparsely clothed with some long hairs on inner margin at base; tibia with a narrow inner apical process defined by an oblique depression on both outer and inner surfaces; tarsus with first segment greatly reduced; second segment much longer than first, claws arising from near base or middle of second segment and with distinct arolium. Middle leg with femur straightly narrowed apically, one and two thirds to twice as long as tibia; armed with spinous bristles sparsely; tibia straightly narrowed apically, about one and a half to almost twice as long as first tarsal segment; first tarsal segment about four and a half to almost eight times as long as second tarsal segment, claws arising from a little beyond middle of second segment. Hind leg also progressively tapering apically; femur straightly narrowed apically, sparsely clothed with spinous bristles, about twice to two and a half times as long as tibia; tibia five to six times as long as first tarsal segment; first tarsal segment nearly as long as to twice as long as second tarsal segment; second segment with slender claws arising from near middle.

Abdomen with first tergite, when recognizable, nearly straight on anterior margin; second and third tergites with anterior margins produced anteriorly, but obliterated medially in majority of species; connexivum slightly reflexed, anterior margin of third connexival segment lost in some species. Anterior ventrites strongly reduced in length. Abdominal spiracles were not studied (abdomen is flanked by metacetabula and hind legs).

Male: Seventh segment ventrally a little shorter or longer than all preceding ventrites together. Eighth segment with dorsal posterior margin broadly rounded. Ninth segment with suranal plate simple, with foot-shaped process at base of lateral margin; pygophore small, apical margin simply rounded; parameres well retained, asymmetrical in *kuiterti*. Endosoma with definitive dorsal plate turned back along apical margin of endosoma, robust and bifurcate at apex (the part of apical plate), basally branched into two slender parallel plates, and fused with basal plate which in turn fused with ventral plate; ventral plate membranous apically; lateral plates simple and elongate. (Description of the genitalia is based on *chinai, malayensis, kuiterti.*)

Female: Seventh segment ventrally a little shorter or longer than all preceding segments together, concave on posterior margin. Eighth segment well exposed ventrally; first valvula with outer lobe acutely pointed at apex, inner lobe fused with vulva; ramus reaching apical third of valvula on its outer margin, basally connected with process of ninth tergite on its outer margin, which is provided with a crescent shaped plate at its apex. Second valvula sclerotized along outer margin, apical lobe membranous and directed mesad apically, with another poorly developed membranous apical lobe above; iutervalvular membrane with its apical margin broadly concave, with a fine dark line above apical margin. Vulva large, broadly rounded on apical margin. (Description of the genitalia is based on *V. kuiterti*).

Winged forms: Pronotum with humeri located much in front of middle of pronotum, nearly straightly narrowed apically from humeri. Hemelytra as in *Metrocoris* but lower cell longer and vein A joined at its extremity. R + M + Cu vein indistinct.

Distribution: The Oriental region (Burma, Ceylon, India, Java, Malaya, Philippines).

Subgenus *Ventidius* Distant *s. str.*

For type designation and citations see generic bibliography.

Body larger. Second antennal segment longer than third segment in majority of species. Front femur simple. Mesosternum simple. Metacetabulum with posterolateral angle simple. Parameres symmetrical.

Subgenus *Ventidioides* Hungerford and Matsuda

Ventidioides Hungerford and Matsuda, Univ. Kansas Sci. Bull. 40(7):333-337 (1960.)

Type species: *Ventidius kuiterti* Hungerford and Matsuda, by original designation.

Body smaller. Second antennal segment shorter than third. Front femur with a tuberculous bump on inner margin in male. Mesosternum with a small tubercle (pore?) led by longitudinal canal internally on median longitudinal axis. Metacetabulum with posterolateral angle with two obtuse projections. Parameres asymmetrical.

The subgeneric distinction lies primarily in the presence or absence of the porous tubercle on the mesosternum. All other characters that characterize *Ventidioides* are evidently more specialized conditions of their counterpart in *Ventidius s. str.* The difference in proportional lengths between the second and third antennal segments probably has been derived from much the same growth mechanism for the segments.

Modification of the abdomen of the male

In the larger species, *malayensis, usingeri,* the seventh segment is distinctly or a little shorter than the five preceding segments together ventrally; in smaller species (*e. g., werneri, kuiterti, henryi*) the seventh segment is relatively long. The eighth segment is largely withdrawn beneath the seventh in *malayensis;* in all other species the eighth segment is more or less greatly prolonged. The parameres are distinct in all species, but they are somewhat reduced in size in the otherwise most primitive species, *malayensis.* The parameres are asymmetrical in the specialized species, *kuiterti.*

Modification of the other structures

The antennae: The second antennal segment is definitely longer than the third segment in both sexes in the larger species, *malayensis* and *usingeri;* in the smaller species the second segment is about as long as or even shorter than the third segment. It is apparent that the length of the second segment in relation to the third has become smaller with reduction in size of the body, and this is due presumably to a greater growth ratio for the second segment than for the third segment common to all species of this genus.

The rostrum: The third rostral segment is about three times as long as the fourth in the larger species, *malayensis* and *usingeri,* but in the smaller species the third segment is definitely less than three times as long as the fourth. As in other genera the length of the third segment in relation to the fourth has evidently become smaller with reduction of the body size in evolution.

Genus *Esakia* Lundblad

(Figs. 44, 854-871)

Esakia Lundblad, Arch. Hydrobiol. Suppl. 12, Tropische Binnengewässer 4:401-405(1933).

Esakia Hungerford and Matsuda, Jour. Kansas Ent. Soc. 31(3):193-197(1958).

Type species: *Esakia ventidioides* Lundblad, monobasic.

Species examined: *E. ventidioides* Lundblad, *E. kuiterti* Hungerford and Matsuda, *E. usingeri* Hungerford and Matsuda.

Color pattern: Predominantly black, with a large pale yellow spot on mesonotum and metanotum and with a whitish spot on mesoacetabulum and metacetabulum in *usingeri.*

Structures in wingless forms: Small and flattened. General shape wider anteriorly than in related genera, such as Ventidius. Head including eyes over twice as wide as long in middle. Eye strongly exserted, extending slightly beyond lateral limit of pronotum, covering a part of mesonotum. Antenna a little longer in male than in female, placed on ventral surface of body; first segment longest, longer than two following segments together, swollen at middle, slightly constricted near apex in some species, apex truncate, sparsely clothed with fine bristles; second segment club shaped, simply and gradually thickened anteriorly, apex truncate, a little shorter than third; *third segment in male strongly flattened, with ear shaped basal peduncle, lateral margin fringed with stiff black hairs; fourth segment fusiform, with inconspicuous basal peduncle and stiff hairs on basal lateral margins.* Rostrum short, nearly reaching posterior margin of prosternum, short and robust; third segment twice or less than twice as long as last segment.

Pronotum short, much shorter than head, posterior margin nearly straight, or feebly concave, lateral margin rounded. Intersegmental suture feebly produced anteriorly, obliterated laterally. Metanotum without median longitudinal sulcus, lateral elevation of metanotum reaching intersegmental suture between mesonotum and metanotum; metacetabular suture evanescent apically, not reaching lateral longitudinal elevation of metanotum. Metasternum highly reduced, represented by a small, transverse, subtriangular plate bearing omphalium. Front leg with tronchanter lacks tubercle; femur considerably longer than tibia, simple; tibia gradually thickened apically, with narrow inner apical process defined by oblique depression on both surfaces; tarsus with first segment very short, second segment with claws arising from near middle, with distinct arolium, several times as long as first segment. Middle leg with femur one and a half to one and two thirds times as long as tibia; tibia about two and a half to about three times as long as first tarsal segment, with a fringe of hairs on inner margin basally; first tarsal segment a little over four times to a little over six times as long as second tarsal segment, claws arising preapically. Hind leg with femur over three times as long as tibia; tibia about six times as long as first tarsal segment; first tarsal segment about two thirds as long as second tarsal segment in most species; second segment with claw arising from a little beyond middle of the segment.

Abdomen has anterior margin of first tergite usually recognizable; anterior margins of second and third tergites roundly produced;

third to sixth tergites subequal in length. Connexivum reflexed. Ventrites much more reduced than tergites.

Male: Seventh segment ventrally about as long as two preceding segments together in *usingeri* or longer in *kuiterti,* concave on ventral apical margin. Eighth segment broadly rounded on apical margin dorsally, broadly concave on ventral apical margin. Ninth segment with suranal plate long and slender; pygophore feebly concave on ventral apical margin; parameres conspicuous and lobate. Endosoma with definitive dorsal plate membranous apically, curved back on apical margin, basally distinct from ventral plate at upper basal angle of endosoma; ventral plate wide and paired, flat apically, curved back along dorsal margin of endosoma; lateral plates located in upper basal half of endosoma; thin U-shaped sclerite goes across apical portion of dorsal plate. (Description of the genitalia is based on *kuiterti.*)

Female: Seventh segment well developed, as long as or a little shorter than all preceding segments together, posterior margin concave. Eighth segment well exposed ventrally, dorsal apical margin produced posteriorly. First valvula thickened apically and acutely pointed at inner apical angle, membranous except on outer margin which is sclerotized, inner lobe infolded beneath outer lobe, shorter and tapering apically. Second valvula with two pairs of apical lobes directed mesad, outer lobe more heavily sclerotized, and superposed on inner lobe which is membranous; short apical margin of intervalvular membrane between inner lobes straight, intervalvular membrane also with an arched, thinly sclerotized slender bar above apical margin; process of ninth-tergite obliquely connected basally with lateral area of ninth tergite.

Winged forms: Pronotum subpentagonal in shape, widest in front of middle in *usingeri.* Forewing coriaceous along upper basal margin. R + M + Cu send a fine oblique branch from middle of the wing to be united with vein A, without forming apical cells.

Distribution: The Oriental region (Burma, Java, Philippines).

This genus is related to *Ventidius* Distant but can be recognized from it by the following characteristics which indicate greater degrees of specialization in *Esakia:*

(1) The forewing venation is more reduced.

(2) The third antennal segment is peculiarly modified in the male.

(3) The presence of the lateral longitudinal elevation of the metanotum reaching the definitive intersegmental suture between the mesonotum and metanotum.

(4) The shape of the body is more widened anteriorly.

SUBFAMILY RHAGADOTARSINAE LUNDBLAD

Rhagadotarsinae Lundblad, Arch. Hydrobiol, Suppl. 12, 4:411-412(1933).
Rhagadotarsinae Hungerford, Univ. Kansas Sci. Bull., 36(1):529-531(1954).

Structures in wingless forms: Head between eyes subquadrangular in shape, dorsal surface usually with a more or less distinct median longitudinal depression; anterior margin with three distinct projections, *i. e.*, median clypeal region and lateral antenniferous tubercles. Clypeus elevated and short, well defined basally. Eye small, inner margin not concave, covering anterolateral angle of pronotum. Antenniferous tubercles well developed. Antenna slender and relatively short, greatly modified in males of many species of *Rheumatobates.* Mandibular and maxillary plates well defined from each other, the latter well developed and produced, forming bucculae, and enclosing base of rostrum. Rostrum slender and relatively short, third segment less than twice as long as last segment.

Pronotum not prolonged, posterior margin concave. Definitive intersegmental suture between mesonotum and metanotum represents posterior margin of mesothoracic postnotum dorsally and laterally metacetabular suture in winged forms, well impressed and broadly roundly produced posteriorly at middle. Mesonotum laterally defined by longitudinal suture. Mesoacetabular region dilated posteriorly. Mesosternum with posterior margin simply concave; paired longitudinal sutures separating mesosternum from mesopleural regions lost. Metathoracic spiracle placed obliquely anterior to definitive intersegmental suture between mesonotum and metanotum, small. Metanotum short, with or without median longitudinal sulcus, laterally defined by first connexival segment. Metacetabular region more or less displaced lateroventrally by first connexival segment which extends anteriorly into metanotal region. Metasternum relatively long; omphalium as well as omphalial groove absent. Front leg with femur slender, about twice as long as tibia; tibia greatly thickened apically, with or without apical projection. First tarsal segment always greatly reduced; second segment with or without longitudinal cleft apically, claws arising from base of cleft in *Rheumatobates.* Middle leg longer than hind leg. *Coxa prolonged* in males of some species of *Rheumatobates; femur and tibia modified in males of many species of Rheumatobates; tarsal segments distinct from each other. Hind leg more or less greatly modified in coxa, trochanter, femur, and tibia in males of many species of Rheumatobates.* First and second tarsal segments distinct from each other.

Abdomen with first segment greatly intruded into metathoracic region. First connexival segment almost reaching or reaching intersegmental suture between mesonotum and metanotum, its posterior margin distinct; first ventrite clearly present behind metasternum; first tergite with anterior margin distinct only laterally. Second to sixth segments subequal in length to each other both dorsally and ventrally.

Winged forms: Hemelytra with R + M + Cu forked into two branches, anterior branches (R + M) either connected or not connected with Sc by oblique cross vein behind middle of hemelytra; posterior branch (Cu) either connected or not connected with A at the middle of hemelytra; the anterior branch apically either fused with Sc to form a cell along anterior margin of hemelytra or not forming a cell. Thinly pigmented line of weakness present. Pronotum with humeri located behind middle, posterior margin broadly rounded.

Male: Seventh segment longer than sixth, its ventral apical margin simply concave, prolonged and longitudinally depressed in *Rhagadotarsus.* Eighth segment simple, prolonged in *Rhagadotarsus.* Ninth segment with suranal plate simple; pygophore with apical margin broadly rounded; parameres absent. Endosoma with apical, dorsal, basal, and ventral plates completely fused together, forming a ring.

Female: Seventh segment with ventral apical margin simply concave. Eighth segment more or less greatly prolonged. *Female genitalia forming complete ovipositor.* Second valvulae completely fused apically to enclose first valvulae; both first and second valvulae are basally connected with black subtriangular region of process of ninth tergite.

Distribution: The Oriental, Ethiopian, Nearctic, and Neotropical regions.

The Rhagadotarsinae is a peculiar group in which some highly primitive characters are combined with some highly specialized characters. As already noted, this subfamily is related to Trepobatinae but the subfamily is more primitive than Trepobatinae in the following characteristics:

(1) The mandibular and maxillary plates are well defined from each other, the latter is especially well developed and forms the bucculae to accommodate the rostrum between. This is peculiar to this subfamily.

(2) The clypeus with the basal margin is well defined; the basal margin is obliterated in most genera of the Trepobatinae.

(3) The antenniferous tubercles are much more well developed than in Trepobatinae.

(4) The mesonotum is provided with the lateral longitudinal suture which defines the mesonotum from the mesopleural region. The suture occurs only in *Potamometra* of Ptilomerinae and few genera of Gerrinae in which the pronotum is not prolonged in wingless forms.

(5) The first connexival segment with the posterior margin is distinct; it is completely obliterated and the segment is almost indistinguishably fused with the metacetabular region in Trepobatinae.

(6) The first ventral abdominal segment is well retained. This is peculiar to this subfamily in the Gerridae.

(7) Associated with the longer body, the metasternum as well as the abdominal segments are longer than in the Trepobatinae.

(8) The female genitalia is the well formed ovipositor. This is peculiar to this subfamily.

(9) The forewing venation is more primitive than that in the Trepobatinae.

The Rhagadotarsinae, however, is more specialized than the Trepobatinae in the following characteristics:

(1) The antennal and leg segments are highly modified in males of many species of *Rheumatobates.*

(2) The omphalium has been completely lost, while it is retained in two genera of the Trepobatinae.

(3) The parameres have been completely lost, while they are retained in a majority of genera of the Trepobatinae.

(4) The endosoma with the apical, dorsal, basal, and ventral plates are completely fused to form a loop; while they are not completely fused in the Trepobatinae.

Evolutionary tendencies in Rhagadotarsinae

At the subgeneric or generic level the more primitive characters are associated with the genus *Rhagadotarsus* or the subgenera of *Rhagadotarsus,* which are larger in size. The maxillary plate and the antenniferous tubercles are most well developed in *Caprivia* which is the largest in size; they are less developed in *Rhagadotarsus s. str.* than in *Caprivia;* least developed in *Rheumatobates* which is the smallest in size. The metasternum and abdominal segments are the longest in *Caprivia* and shortest in *Rheumatobates.* The modification of the antennal and leg segments has arisen only in *Rheumatobates* which is smallest in body size. It may thus safely be concluded that the structures have become more specialized with reduction of body size at the subgeneric and generic level in evolution of the Rhagadotarsinae.

At the species level, however, this relation is reversed in *Rheumatobates.* As will be noted from the following table the species with more specialized antennal and leg segments in males are generally greater in body length than the species without or with a slight modification of the antenna and legs. This tendency is much more pronounced in the male than in the female. It should be also noted that the two species belonging to the subgenus *Hynesia* of *Rheumatobates* do not conform to this tendency.

Genus *Rhagadotarsus* Breddin

(Figs. 37, 38, 123, 141, 161, 168, 881-903)

Rhagadotarsus Breddin, Mitt. Nat. Mus. Hamburg, 22:137(1905).
Rhagadotarsus Bergroth, Philip. Jour. Sci., 13:122(1918).
Rhagadotarsus Lundblad, Arch. Hydrobiol., Suppl. 12:412-414(1933).
Nacebus Distant, Ann. Mag. Nat. Hist., 8(5):165(1910) (type species, *Nacebus dux* Distant).

Type species: *Rhagadotarsus kraepelini* Breddin, monobasic.

Species examined: *R. (R.) kraepelini* Breddin, *R. (C.) hutchinsoni* China.

Color pattern: Black in ground color. Head along eyes and posterior margin reddish. Pronotum yellow to orange yellow at middle. Both mesonotum and abdominal tergites largely whitish black. Coxae, trochanters, and basal regions of femora paler. Body beneath concolorous with body above.

Structures in wingless forms: Head with an obscure median longitudinal sulcus or sometimes without it, posterior margin concave. Antenniferous tubercles especially well developed in subgenus *Caprivia,* in which they reach almost to tip of clypeus. Antenna slen-

TABLE 14.—Lengths of body in species of *Rheumatobates*.

	Length of body	
	Male	Female
Without modification in males:		
R. petilus	1.89–2.3 mm.	2.55–2.77 mm.
R. drakei	1.728 mm.	....
R. bonariensis	1.89–2.1 mm.	2.25–2.52 mm.
R. minutus	1.6 mm.	....
R. minutus flavidus	1.6–1.89 mm.	1.785–2.2 mm.
R. vegatus	2.0–2.24 mm.	2.68–2.95 mm.
The front leg only modified in males:		
R. clanis	2.1–2.38 mm.	2.37–3.17 mm.
R. mangrovensis	2.8 mm.	3.3 mm.
R. trinitatis	3.1 mm.	3.7 mm.
The hind and middle legs modified and third antennal segment unmodified in males:		
R. klagei	2.27–2.52 mm.	2.8–3.0 mm.
R. crassifemur crassifemur	2.0–2.22 mm.	2.5–2.86 mm.
R. crassifemur schroederi	2.02–2.4 mm.	2.52–3.15 mm.
R. crassifemur esakii	2.05–2.39 mm.	2.5–2.94 mm.
The hind and middle legs modified and the third antennal segment modified in males:		
R. carvalhoi	2.9–3.0 mm. (for male and female?)	
R. creaseri	2.55 mm.	2.9 mm.
R. citatus	2.52 mm.	2.52–2.69 mm.
R. praeposterus	2.02–2.2 mm.	2.56–2.9 mm.
R. hungerfordi	2.6–2.94 mm.	2.73–3.25 mm.
R. trulliger	2.5–2.8 mm.	2.73–3.15 mm.
R. tenuipes	2.44–2.86 mm.	2.94–3.28 mm.
R. spinosus	1.785 mm.	....
R. mexicanus	2.18–2.52 mm.	2.7–2.86 mm.
R. rileyi	2.2–2.5 mm.	2.64–3.15 mm.
R. rileyi paloisi	2.7–2.94 mm.	2.64–3.36 mm.
R. bergrothi	2.3–2.94 mm.	2.64–3.46 mm.
R. imitator	2.31–2.6 mm.	2.73–2.94 mm.
R. meinerti	2.52 mm.	3.06 mm.

The length of body is after Hungerford (1954).

der; first segment much longer than second; second segment always shorter than third; third segment slender; fourth segment slender, about as long as third or longer. Eye small, covering only anterolateral angle of pronotum posteriorly. Mandibular and maxillary plates well defined from each other, the former small, the latter well developed and produced anteriorly on each side of rostrum, thus forming bucculae. Rostrum rather short, basally telescoped between bucculae; third segment less than twice as long as last segment.

Pronotum very short, basal margin concave, lateral margin rounded, narrower than head including eyes. Intersegmental suture between mesonotum and metanotum produced posteriorly at middle. Mesonotum laterally defined by longitudinal suture which extends entire length of mesonotum, median longitudinal sulcus more or less distinct throughout entire length of mesonotum. Mesoacetabular region strongly dilated laterally. Mesosternum broadly concave on apical margin. Metanotum short, with or without a more or less distinct median longitudinal sulcus. Metasternum slightly depressed near anterior margin, posterior margin concave, less than half as long as mesosternum. Front leg with coxa short; femur slender and without sexual difference in shape, slightly thickened apically; tibia strongly narrowed basally, less than half as long as femur, apical margin concave, flattened, shallowly depressed on inner surface in apical half; tarsus with first segment greatly reduced, second segment rather thick, rounded especially on anterior margin; apical half splits into two parts by cleft, anterior part thicker than posterior part; claws arising from base of the cleft, with distinct membranous arolium. Middle leg with coxa short; femur slender and straight, subequal in thickness throughout, over one and one fifth times as long as tibia; tibia more slender than femur, about two and one fifth (*Rhagadotarsus s. str.*) to a little less than three times (*s. g. Caprivia*) as long as first tarsal segment. First tarsal segment one and a half to two and a half times as second segment; second segment with apical hairs and claws arising from near apex. Hind leg with coxa relatively long; femur a little over twice as long as (*Rhagadotarsus s. str.*) or about two and a half times as long as tibia (*s. g. Caprivia*); tibia about five times as long as first tarsal segment; first tarsal segment as long as or a little shorter than second segment; second segment with claws arising from a little beyond middle of second tarsal segment.

Abdomen long, nearly straightly narrowed posteriorly. First abdominal tergite with anterior margin distinct only laterally; second to fifth tergites subequal in length. Connexivum rather strongly reflexed. First connexival segment with posterior margin distinct, anteriorly nearly reaching intersegmental suture between mesonotum and metanotum. Ventrites subequal in length throughout second to sixth segments, with a shallow laevigate depression on each segment in male; first ventrite broadly rounded on anterior margin and a little longer than second ventrite. Abdominal spiracles placed closer to posterior margin than to anterior margin or at middle between anterior and posterior margins.

Male: Seventh segment longer than sixth segment both dorsally and ventrally, straight on apical margin dorsally, or concave ventrally, with a rather deep depression ventrally. Eighth segment cylindrical, over twice as long as seventh segment, strongly longitudinally depressed ventrally. Ninth segment with suranal plate simple, elevated longitudinally; pygophore with apical margin simply rounded; parameres absent. Endosoma with apical, dorsal, basal, and ventral plates completely fused, forming a loop and extends beyond apex of endosoma; lateral plates small and inconspicuous. (Description of the genitalia is based on *R. (R.) kraepelini.*)

Female: Seventh segment much longer than sixth segment, concave on ventral apical margin. Eighth segment cylindrical. Valvifers narrowed apically, extending beyond apical margin of eighth tergite. First valvula well sclerotized, simply narrowed apically and with acute tip, basally connected with a subtriangular part at apex of ninth tergal process, which is membranous and long. Second valvulae completely fused apically, forming a complete sheath and with acute tip; ramus very fine but distinct as far as near apex of valvula, connected basally with tip of black plate at apex of ninth tergal process. Ninth tergite slender, slightly thickened at middle, with round apical margin. (Description of the genitalia is based on *R. (R.) kraepelini* and *R. (C.) hutchinsoni.*)

Winged forms: Hemelytra with R + M + Cu forked into two branches, anterior branch connected with Sc by an oblique vein at the point behind middle of hemelytra, and apically fused with Sc; posterior branch connected with A at the middle of hemelytra; a rather obscure straight line of weakness recognizable at middle of apical half of hemelytra. Vein A connected with rear margin of hemelytra by a short oblique vein. Hind wing as in fore wing, but upper (anterior) branch of R + M + Cu not fused with Sc apically, and A not connected with posterior margin of wing by a short cross vein.

Distribution: The Oriental region (Burma, China, Formosa, India, Java, Philippines, Malaya) for *Rhagadotarsus s. str.*, and the Ethiopian region (South Africa, French Congo, Belgian Congo, Sudan) for *Caprivia.*

Rhagadotarsus s. str. and the subgenus *Caprivia* can be distinguished by comparing the following description for each subgenus.

Subgenus *Rhagadotarsus* Breddin *s. str.*

For type designation and citations see generic bibliography.

Body relatively short. Bucculae and antenniferous tubercles relatively weakly developed. Middle tibia a little over twice as long as first tarsal segment. Hind femur a little over twice as long as first tarsal segment.

Subgenus *Caprivia* China

Caprivia China, Ann. Mag. Nat. Hist., 10(8):408(1931) (as a subgenus of *Rhagadotarsus*).

Type species: *Rhagadotarsus hutchinsoni* China, by original designation.

Body almost cylindrical. Bucculae and antenniferous tubercles well developed. Middle tibia a little less than three times as long as first tarsal segment. Hind femur about two and a half times as long as tibia.

Genus *Rheumatobates* Bergroth

(Figs. 39, 123, 141, 161, 168, 904-961)

Rheumatobates Bergroth, Insect Life, 4:321(1892).
Rheumatobates Schroeder, Univ. Kansas Sci. Bull., 20(2):63-99(1931).
Rheumatobates Hungerford, Univ. Kansas Sci. Bull., 26(1):529-588(1954).
Hymenobates Uhler, Proc. Zool. Soc. London, p. 214(1894) (type species, *Hymenobates imitator* Uhler).
Halobatopsis Ashmead, Canad. Ent., 29:56(1897) (in part, nec Bianchi 1896).
Telmatobates Berg, Comm. Mus. Nac. Buenos Aires, 1(1):5-6(1898) (type species, *Telmatobates bonariensis* Berg).
Hynesia China, Proc. Roy. Ent. Soc. London, (B)12(5-6):71-72(1943) (type species, *Hynesia trinitatis* China).

Type species: *Rheumatobates rileyi* Bergroth.

Species examined: *R. bergrothi* Meinert, *R. bonariensis* (Berg), *R. clanis* Drake and Harris, *R. carvalhoi* Drake and Harris, *R. citatus* Drake and Hottes, *R. crassifemur crassifemur* Esaki, *R. crassifemur esakii* Schroeder, *R. crassifemur schroederi* Hungerford, *R. creaseri* Hungerford, *R. drakei* Hungerford, *R. hungerfordi* Wiley, *R. imitator* (Uhler), *R. klagei* Schroeder, *R. mangrovensis* (China), *R. meinerti* Schroeder, *R. mexicanus* Drake and Hottes, *R. minutus flavidus* Drake and Harris, *R. petilus* Drake and Hottes, *R. praeposterus* Bergroth, *R. rileyi* Bergroth, *R. rileyi palosi* Blatchley, *R. tenuipes* Meinert, *R. trinitatis* (China), *R. trulliger* Bergroth, *R. vegatus* Drake and Harris.

Color pattern: Predominantly black. Pronotum ochraceous except sides black. Head reddish brown along basal margin. Mesonotum occasionally with an ochraceous spot. Legs with middle and hind coxae and trochanters ochraceous. Connexivum occasionally totally ochraceous or laterally ochraceous. Body beneath usually paler.

Structures in wingless forms: Head with an obscure median longitudinal impression usually recognizable in anterior half of uppersurface. Antenniferous tubercles more well developed in males than in females of some species in which antennae greatly modified. Antenna in female short and slender in all species; first segment shorter than second and third segments together, second segment shortest, third one usually with two long hairs arising from apex and near middle of inner margin; fourth segment fusiform. Antennae in males highly variable in shape and proportional lengths of segments, greatly modified in many species. Mandibular and maxillary plates clearly separted from each other, the latter well developed and rounded on upper apical margin. Rostrum slender, relatively short; third segment usually about twice as long as fourth segment.

Pronotum longer in males than in females in some species, strongly produced posteriorly on each side, posterior margin concave. Intersegmental suture between mesonotum and metanotum broadly convex dorsally. Mesonotum laterally defined from mesopleural regions by a longitudinal suture; median longitudinal sulcus distinct; mesoacetabular region dilated. Mesosternum broadly concave on apical margin. Metanotum short, median longitudinal sulcus often absent, laterally defined by first abdominal connexival segment which intrudes anteriorly into metanotal region; metacetabular region somewhat displaced lateroventrally by first connexival segment. Metasternum about half as long as mesosternum, posterior margin less concave than anterior margin. Front leg in female with simple and slender femur and short and thick tibia. Front leg in male with femur sparsely clothed with long hairs on inner margin, strongly thickened and with some black long hairs in some species; tibia about half as long as femur, rather strongly thickened apically, inner apical angle lobately produced; tarsus a little shorter than tibia; first segment greatly reduced and basally hidden under hairy apical margin of tibia; second segment rounded on anterior margin, apex acute and without cleft, long claws arising from near middle of inner margin. Middle leg with femur and tibia have a row of long hairs on inner margin in males of some species, and the former thickened apically or curved and peculiarly thickened in males of some species; femur longer than tibia in most species; tarsus with first segment a little less than twice to a little over three times as long as second segment in females; second segment with small claws arising from beyond middle. *Hind leg greatly modified from coxa to tibia in males of some species.* Femur over one and a half times as long as tibia in most species. First tarsal segment shorter than second in females of all species, or much longer than second in males of some species in which the preceding segments are greatly modified; second tarsal segment with well developed long claws.

Abdomen obovate. Anterior margin of first tergite roundly produced anteriorly, usually obliterated medially. First segment greatly encroaching into metathoracic region pleurosternally; first connexival segment with posterior margin distinct and at about the same level as first abdominal spiracle, anteriorly reaching definitive intersegmental suture between mesonotum and metanotum, ventrally first ventrite clearly retained and longer than second abdominal ventrite. Second to sixth segments subequal in length both dorsally and ventrally, anterior margin of second tergite slightly produced anteriorly.

Male: Seventh segment longer than sixth, simple on ventral apical margin. Eighth segment rather strongly drawn out and more or less cylindrical. Ninth segment with pygophore rounded on apical margin; parameres absent. Endosoma with apical, dorsal, basal and ventral plates completely fused, forming a loop, not extending beyond apex of endosoma apically, with small lateral plates. (Description of the genitalia is based on *R.* (*R.*) *crassifemur.*)

Female: Seventh abdominal segment with ventral apical margin concave. Eighth segment strongly prolonged. First valvula long, acutely pointed, inner lober darker basally, with a fine apical process almost reaching near apex of outer lobe; ramus connected with a dark subtriangular plate basally. Second valvulae fused apically, forming a narrow sheath to enclose first valvulae within, connected basally with black subtriangular region of the process from ninth tergite on its inner margin. (Description of the genitalia is based on *R. (R.) crassifemur.)*

Winged forms: Hemelytra with R + M + Cu connected with Sc by an oblique vein at basal third, anterior branch not connected with Sc apically; posterior branch apically not connected with A. Vein A extending only in basal third. T-shaped white line of weakness spreading in apical two thirds of hemelytra. *Hind wing venation as in forewing venation, much more reduced than in Rhagadotarsus.*

Distribution: The Western Hemisphere (Large part of the United States, Argentina, Brazil, British Guiana, British Honduras, Cuba, Mexico, Paraguay, Panama, Peru, Pureto Rico).

The genus *Rheumatobates* is distinguishable from *Rhagadotarsus* by the following characters:

(1) The wing venation is more reduced, *i. e.,* the apical cell is not formed and the line of weakness is T-shaped, while in *Rhagadotarsus* the hemelytra with its venation is more developed and forms an apical cell along the anterior margin of the wing, and the whitish line of weakness is simply horizontal.

(2) The second tarsal segment of the front leg is without cleft, whilst it is split into two parts by a narrow longitudinal cleft in *Rhagadotarsus.*

(3) *Rheumatobates* is obviously much more specialized than *Rhagadotarsus* as seen in the higher degrees of specialization in the antennae and legs in males of many species.

The genus *Rheumatobates* is divided into two subgenera, *i. e., Rheumatobates s. str.* and *Hynesia* China. The differences between the two subgenera are only in the males.

Subgenus *Rheumatobates* Bergroth *s. str.*

For type designations and citations see generic bibliography.

Male antennal segments greatly modified in most species. Fourth antennal segment at least not much longer than third. Male front leg with femur modified but not much thickened and without a row of conspicuous spines on entire inner margin.

Subgenus *Hynesia* China

Hynesia China, Proc. Roy. Ent. Soc. London, Ser. B, 12(5-6):71-72(1943) (as genus).
Hynesia Hungerford, Univ. Kansas Sci. Bull., 36(1):534 (as subgenus).

Type species: *Hynesia trinitatis* China, by original designation.

Male antennae long, not greatly modified; fourth antennal segment very long in *trinitatis.* Male front femur much longer and thicker than in *Rheumatobates s. str.*, with a row of conspicuous spines on entire inner margin.

Two species, R. (*H.*) *trinitatis* (China) and R. (*H.*) *mangrovensis* (China) from Trinidad belong to this subgenus.

SUBFAMILY TREPOBATINAE MATSUDA

Structures in wingless forms: Relatively homogeneous, highly specialized group including thirteen genera of small body size. Shape of body elliptical or sometimes globular.

Head with anterior margin more or less broadly rounded in dorsal view. Clypeus with basal margin either obliterated or retained. Eye not entirely covering lateral margin of pronotum, more or less rounded on inner margin. Antenniferous tubercles scarcely or poorly developed. Antennal cavities open anterior to eyes. Antenna slender; first segment longest in most genera, strongly incrassate in males of *Metrobatopsis;* relative lengths between second and third segments vary considerably in various genera, second and third modified distally in *Metrobates;* fourth segment as long as or longer than third in most genera. Mandibular and maxillary plates distinct from each other in some genera. Rostrum relatively short, third segment not over three times as long as last.

Pronotum never prolonged, shorter and narrower than head in many genera. Intersegmental suture between mesonotum and metanotum represented dorsally by posterior margin of metathoracic postnotum in winged forms, and laterally by metacetabular suture in winged forms. Mesonotum with or without median longitudinal sulcus; lateral longitudinal suture defining mesonotum from mesopleuron absent. Mesosternum with paired longitudinal suture defining mesosternum from mesopleuron absent in all genera. Metathoracic spiracle inconspicuous, placed subparallel with intersegmental suture between mesnontum and metanotum laterally. Metanotum with median longitudinal sulcus absent in most genera. Metacetabular region dilated posteriorly, elevated as far as the intersegmental suture anteriorly. Metasternum a little longer than second abdominal ventrite in most genera; omphalium absent in most genera. Front leg with femur modified in some species of some genera; tibia without conspicuous process at inner apical angle, modified in males of some species; tarsus with first segment greatly reduced; second segment often several times as long as first, claws arising from near middle of second segment. Middle leg longer than hind leg; femur thick and short; tibia always longer than femur, about twice as long as femur in some genera; tarsus with first segment always longer than second except for *Metrobates,* in which second segment longer than first. Hind leg with femur always longer than middle femur and than hind tibia; tarsus with first and second segments fused in some genera, second segment much longer than first and with conspicuous claws in *Metrobates*.

Abdomen has anterior margins of first and second tergites obliterated in some genera, broadly rounded when recognizable, both segments much longer than third tergite. First ventrite absent; ventrites more reduced than tergites, but less than in Halobatini. Connexivum extends into well elevated metacetabular region and indistinguishably fused with the latter in some genera, nearly horizontal or slightly reflexed in most genera. Abdominal spiracles, when recognized, located at middle or a little closer to posterior margin than to anterior margin of segments.

Male: Seventh segment with ventral apical margin simply concave or nearly horizontal. Eighth segment dorsally more well developed, more or less greatly prolonged in some genera. Ninth segment with suranal plate armed with a spinous process directed cephalad apically on each lateral margin in some genera. Pygophore simple in great majority of genera; parameres retained in most genera and simple. Endosoma with dorsal plate apically either fused with or distinct from apical plate; basal and ventral plates absent in most genera, they are weakly developed when present; lateral plates sometimes not well defined.

Female: Seventh segment ventrally longer than sixth; ventral apical margins simply concave or nearly horizontal in great majority of species; apical tergites modified in some species of *Metrobatopsis.* Eighth segment well exposed in some genera. First valvula with inner lobe always folded beneath outer lobe, always well pigmented, typically with two apical processes of different length, or they are lost in some genera; ramus of first valvula pigmented, located typically along outer margin of process of ninth tergite. Second valvula long, rounded apically, extending beyond apical margin of intervalvular membrane. Vulva relatively well developed, often extending beyond middle of first valvula; ramus fine and long.

Winged forms: Hemelytra long, basal half to one third coriaceous, forming embolium along anterior margin of hemelytron. R + M + Cu forked into two oblique branches near extremity of basal coriaceous area, upper one united with lower apical angle of basal coriaceous area, then together sending a straight vein into apical membranous region, lower branch united with A near extremity of basal coriaceous region, then send a lower straight vein into

TABLE 15.—Table of significant generic characters in Trepobatinae.

	Metrobates	Trepobates	Trepobatoides	Telmatometra	Halobatopsis	Ovatametra	Rheumatometroides	Stenobates	Naboandelus	Cryptobates	Hynesionella	Rheumatometra	Metrobatopsis
7....	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(—)	(+)	(+)	(+)	(+)	(+)
9....	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(+)	(+)	(+)	(+)	(+)
11....	(+)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(+)	(—)	(+)	(—)
19....	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(±)×
22B..	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
28....	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
31....	(+)	(+)	(+)	(+)	(+)	(+)	(—)*	(+)	(+)	(+)	(+)	(±)	(+)
32B..	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(+)	(+)
38....	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(—)	(+)	(+)	(+)	(+)	(+)
39B..	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(+)	(+)	(+)	(+)	(+)
41....	(—)	(—)	(—)	(—)	(—)	(—)	(+)	(+)	(—)	(—)	(—)	(—)	(—)

TABLE 15.—Table of significant generic characters in Trepobatinae—*Continued.*

	Metrobates	Trepobates	Trepobatoides	Telmatometra	Halobatopsis	Ovatametra	Rheumatometroides	Stenobates	Naboandelus	Cryptobates	Hynesionella	Rheumatometra	Metrobatopsis
49....	(+)	(±)×	(+)	(±)×	(±)×	(±)×	(+)	(+)	(±)×	(—)	(±)×	(—)	(—)
54....	(+)	(+)	(+)	(±)	(±)	(±)	(+)	(+)	(+)	(—)	(+)	(+)	(+)
57....	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(?)	(+)	(+)	(+)	(+)	(±)×
62A..	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(?)	(±)	(+)	(+)	(+)	(—)
63B..	(—)	(+)	(—)	(—)	(—)	(—)	(—)	(—)	(?)	(—)	(—)	(+)	(—)
68A..	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(—)	(?)	(+)	(—)	(+)	(—)
69A..	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(?)	(+)	(—)	(±)	(—)
72B, 75B..	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(?)	(+)	(+)	(+)	(—)
90....	(+)	(+)	(+)	(+)	(+)	?	?	?	(—)	(+)	?	(—)	(—)
101....	(±)×	(+)	(+)	(±)	(+)	(+)	(+)	(+)	(+)	(+)	(—)	(—)	(—)

TABLE 15.—Table of significant generic characters in Trepobatinae—*Concluded.*

	Metrobates	Trepobates	Trepobatoides	Telmatometra	Halobatopsis	Ovatametra	Rheumatometroides	Stenobates	Naboandelus	Cryptobates	Hynesionella	Rheumatometra	Metrobatopsis
110....	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
115....	(—)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
126....	1.48–2.02 :1	1.51–1.99 :1	1.45–1.56 :1	1.38–1.57 :1	1.37–1.50 :1	1.55–1.68 :1	1.21–1.24 :1	1.20:1	1.33–1.50 :1	1.18–1.33 :1	1.43–1.47 :1	1.49–1.55 :1	1.33–1.47 :1
127....	0.46–0.81 :1	0.95–1.45 :1	1.73–1.92 :1	1.19–1.54 :1	1.25–1.60 :1	1–1.25 :1	1–1.07 :1	1.19:1	1.33–1.40 :1	1.14–1.64 :1	1–2.46 :1	2:1	2.1–2.75 :1
128....	0.30–0.43 :1	0.45–0.55 :1	0.45–0.50 :1	0.40–0.55 :1	0.47–0.59 :1	0.50–0.59 :1	0.40:1	0.35:1	0.39–0.41 :1	0.39–0.47 :1	0.43–0.50 :1	0.44–0.60 :1	0.33–0.47 :1
129....	0.19–0.35 :1	1.22–1.83 :1	0.83–0.86 :1	0.8–1.14 :1	0.90–1.36 :1	1.11–1.50 :1	0.54–0.60 :1	0.66:1	0.45–0.63 :1	0.8–1:1	0.33–0.48 :1		
Total..	(+) 15 (±) 1 (—) 7	(+) 19 (±) 1 (—) 3	(+) 19 (—) 4	(+) 16 (±) 3 (—) 4	(+) 17 (±) 2 (—) 4	(+) 16 (±) 2 (—) 4 ? 1	(+) 14 (—) 8 (?) 1	(+) 13 (—) 7 (?) 3	(+) 14 (±) 2 (—) 3 (?) 4	(+) 19 (—) 4	(+) 14 (±) 1 (—) 7 (?) 1	(+) 17 (±) 2 (—) 4	(+) 11 (±) 2 (—) 10

* For the female only.

For the explanations of symbols see introduction and table 5.

apical membranous region (this vein is obliterated in *Metrobatopsis*). Line of weakness always present between the two apical straight veins in membranous region.

Distribution: Temperate and tropical zones of the Eastern and Western Hemispheres.

Relationships of genera

As noted from the table of characters, the number of primitive characters varies relatively little among genera in comparison with other subfamilies, indicating a relatively high degree of homogeneity of the subfamily. Derivation of certain genera from certain other existing genera is hard to conceive in this subfamily. Another important fact is that no one genus occurs in both the Eastern and the Western Hemispheres. The distribution of *Metrobates, Telmatometra, Trepobatoides, Trepobates, Halobatopsis* and *Ovatametra* is confined to the Western Hemisphere; *Hynesionella, Metrobatopsis, Rheumatometra, Rheumatometroides, Stenobates, Cryptobates,* and *Naboandelus* occur solely in the Eastern Hemisphere.

Among the genera from the Western Hemisphere, *Metrobates* is unique in the highly flattened body, the modified antennae, the long middle tibia and hind femur, etc., and it is not closely related to any one genus from the Western Hemisphere. *Telmatometra* is more closely related to *Halobatopsis* than to *Trepobates,* as is indicated mainly by a similar proportional lengths of leg segments. *Ovatametra* has possibly been derived from *Telmatometra* or *Halobatopsis* like ancestor with reduction in the body size, etc. *Trepobatoides* is structurally similar both to *Telmatometra* and *Trepobates;* it is, however, quite distinct from both of them by its different proportional lengths of the antennal and leg segments.

Among the genera from the Eastern Hemisphere, *Stenobates* and *Rheumatometroides* are evidently closely related, as indicated by the retention of the omphalium, the metacetabula being dorsally convergent, etc. These characters are peculiar to these genera. *Rheumatometroides* has been known from the Solomon Islands and *Stenobates* from Singapore. *Metrobatopsis* and *Rheumatometra* are known from New Guinea, the Solomon Islands, and Northern Australia. They are not closely related. *Rheumatometra* is similar to *Metrobates* from the Western Hemisphere in certain characters, such as the shape of the body, retention of the median longitudinal sulcus on the mesonotum, the wide head, a similar female genitalia, etc., although both genera are quite distinct from each other by certain specialized characters peculiar to each one of them. *Cryptobates* is relatively more generalized and similar to *Telmatometra* from the Western Hemisphere, especially in the proportional lengths of antennal and leg segments. It is, however, distinct from *Telmatometra* by the complete loss of the anterior margins of the first and second abdominal tergites, etc. *Naboandelus* may be somewhat closely related to *Hynesionella,* although its phylogenetic position is obscure to me because of the absence of the male specimens available for study. *Hynesionella* has hitherto been known only from Africa. The genus is unique in having the carinate definitive intersegmental suture between the mesonotum and metanotum; the modification of the male apical segments is also peculiar, although the suranal plate is provided with a spinous process on the lateral margin as in the other three genera of this subfamily.

Although the intergeneric relationships are often obscure, the following diagram 9 indicating the relationships of genera is tentatively presented:

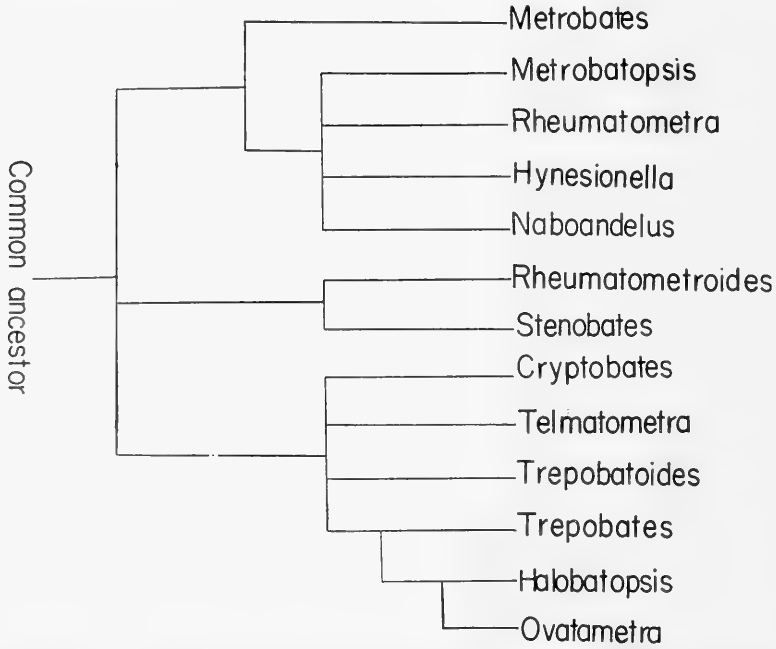

DIAGRAM 9.—Diagram showing the relationships of genera of the Trepobatinae.

Evolutionary tendencies and some structural peculiarities in Trepobatinae

As noted elsewhere, the subfamily is rather highly homogenous and well defined. There is, however, no good evidence to indicate that certain genera have been derived from other existing genera, and the great majority of genera have attained independently about the same degree of structural specialization. It is thus relatively difficult to discuss the process of evolution of structures at the generic level. The following points, however, appear to deserve noting as evolutionary tendencies and structures more or less peculiar to this subfamily.

(1) The relatively short and thick middle femur, which is always shorter than the middle tibia, has been well fixed in this subfamily. This relatively short femur is apparently realized by the smaller growth ratio and smaller initial growth index for the femur than those for the tibia ($P<0.05$ in *Trepobates knighti*).

(2) The growth ratio for the first antennal segment is relatively high. Because of this there is a tendency for this segment to vary greatly in length among the related species without great difference in the body length.

(3) The spinous process on the lateral margin of the suranal plate of the male has arisen in four genera, and the apex of the process is directed cephalad.

(4) The seventh abdominal segment has remained relatively simple, though prolonged. Conspicuous modification of the segment has arisen only in females of certain species of *Metrobatopsis*.

Genus *Trepobates* Uhler

(Figs. 60, 110, 124, 142, 162, 169, 962-980)

Trepobates Uhler, Proc. Zool. Soc. London, p. 213(1894).
Trepobates Kirkaldy, Trans. Amer. Ent. Soc., 32:156(1906).
Trepobates Kirkaldy and Torre-Bueno, Proc. Ent. Soc. Washington, 10:212 (1908).
Trepobates Bergroth, Ohio Nat., 8:373(1909).
Trepobates Torre-Bueno, Trans. Amer. Ent. Soc., 37:245(1911).
Trepobates Hungerford, Univ. Kansas Sci. Bull., 31:114, 119(1919).
Trepobates Esaki, Ann. Mus. Nat. Hung., 23:139(1926).
Trepobates Drake and Harris, Brooklyn Ent. Soc., 27(2):113-123(1932).
Trepobates Drake and Harris, Psyche, 39(4):112(1932).
Trepobates Kenaga, Jour. Kansas Ent. Soc., 15(4):137(1942).
Trepobates Drake and Hottes, Great Basin Nat., 12(1-4):35-38(1952).
Stephania Buchanan-White, Challenger Rept. Zool., 7(19):78(1933) (preoccupied, type species, *Halobates pictus* Herrich Schaeffer).
Kallistometra Kirkaldy, Entomologist, 32:28(1899) (type species, *Kallistometra taylori* Kirkaldy).

Type species: *Halobates pictus* Herrich Schaeffer, by original designation.

Species examined: *T. floridensis* Drake and Harris, *T. inermis* Esaki, *T. knighti* Drake and Harris, *T. pictus* (Herrich-Schaeffer), *T. subnitidus* Esaki, *T. taylori* (Kirkaldy), *T. trepidus* Drake and Harris, *T. vazquezae* Drake and Harris, two unidentified species.

Color pattern: Variegated yellow (or rarely orange yellow) and black. Head usually with a median longitudinal black stripe. In some species the dark markings on dorsal surface are greatly reduced or partially obliterated, whereas in others the color is almost entirely black, the yellow being replaced by black. Mesothorax typically with a median and two pairs of lateral longitudinal black stripes.

Structures in wingless forms: Body oval, moderately pubescent. Head between eyes widened posteriorly, posterior margin nearly straight. Eye exserted, covering anterolateral angle of pronotum. Antennal cavities open cephaloventrad, located on or just above the lines across anterior margins of eyes. Antenna slender, extending back beyond middle of body. First segment longest, a little shorter than second and third segments together; second segment shortest in most species, relative length of second to first greater in female than in male; third segment a little longer than second, third segment in males of some species with long pilosities on lower margin, both second and third segments slightly and simply thickened anteriorly and truncate at apices; fourth segment about as long as or a little longer than third. Mandibular and maxillary plates indistinguishably fused. Rostrum rather slender, reaching mesosternum, third segment about twice as long as last segment in most species.

Pronotum transverse subquadrangular in shape, narrower than head including eyes, posterior margin broadly concave or nearly straight. Mesonotum without distinctly impressed median longitudinal sulcus, a little over twice as long as pronotum in most species. Intersegmental suture between mesonotum and metanotum nearly straight dorsally. Metanotum without distinct median longitudinal sulcus, laterally defined by longitudinal elevation continuous from abdominal connexivum, reaching intersegmental suture between mesonotum and metanotum. Metasternum with omphalium as well as omphalial groove completely lost, longer than second ventrite, less than one tenth as long as mesosternum. Front leg relatively long; femur curved, depressed and concave on inner margin in male; tibia simple, considerably shorter than femur; tarsus with first segment extremely reduced, second segment often several times as long as first segment, claws arising from beyond middle and with fine arolium. Middle leg with femur much thicker than tibia, ciliated on lower margin in males, a little over half as long as tibia; tibia a little over three times as long as first tarsal segment; tarsus with first segment a little longer than second segment in most species, second segment with small claws. Hind leg with femur much more slender but much longer than middle femur, about twice as long as tibia; tibia over twice as long as first tarsal segment; first tarsal segment less than twice as long as second segment.

Abdomen gradually narrowed posteriorly. Connexivum strongly reflexed, especially so in female. First and second abdominal tergites with anterior margins strongly produced anteriorly, anterior margin of first often obliterated medially. Ventrally haired in some species.

Male: Seventh segment much longer than sixth segment and broadly concave on ventral apical margin. Eighth segment about as long as seventh or longer than seventh ventrally, ventral apical margin concave, with a feeble median notch or simply concave on dorsal apical margin. Ninth segment with suranal plate largely hidden beneath eighth tergite, simply rounded on apical margin; pygophore exposed in apical half, broadly rounded on apical margin; parameres robust and simply curved upward apically. Endosoma with dorsal plate turned backward apically, distinctly split into two arms basally; basal plate separated from base of dorsal plate; ventral plate short and membranous, strengthened by black slender sclerite arising from basal plate; lateral plates long and simple. (Description of the genitalia is based on *knighti* and *trepidus.*)

Female: Seventh segment much longer than sixth segment ventrally, broadly concave on apical margin in most species, with long and straight pilosity on apical margin in some species; connexivum strongly reflexed on dorsum, with spinous process apically in *knighti.* Eighth segment with apical half exposed. First valvula with inner lobe dark, split into two lobes, outer one of them almost reaching apex of outer lobe; outer lobe clothed with straight oblique hairs basally, apex membranous, roundly folded; ramus extending along outer margin of process of ninth tergite, which is provided with dark arched crescent shaped sclerite apically. Second valvulae with apices roundly folded and convergent apically; ramus slender, extending basally along ramus of first valvula. Vulva membranous, acutely pointed. (Description of the genitalia is based on *knighti.*)

Winged forms: Hemelytra with well formed embolium. R + M + Cu vein sends short branches both anteriorly and posteriorly, anterior branch connected with Sc and extends into apical membranous region, posterior branch united with vein A at extremity of basal coriaceous region. T-shaped line of weakness recognized basally along apical margin of coriaceous region, and horizontally at middle between two veins in membranous region and reaches apex of hemelytra. Hind wing with Sc connected by oblique branch from R + M at middle, with two apical veins evanescent apically; Cu vein obscure, apically fused with A beyond middle of hind wing. Pronotum widest at middle or a little behind middle.

Distribution: Canada, greater part of the United States, West Indies, Central and South America (Guatemala, Mexico, Panama, Peru, Venezuela).

Genus *Telmatometra* Bergroth

(Figs. 59, 80-81, 125, 142, 143, 169, 981-991)

Telmatometra Bergroth, Ohio Nat., 8:374(1908).
Telmatometra Esaki, Ann. Mus. Nat. Hung., 23:133(1926).
Telmatometra Kenaga, Univ. Kansas Sci. Bull., 27(1):169-183(1941).

Type species: *Telmatometra whitei* Bergroth, *monobasic.*

Species examined: *T. acuta* Kenaga, *T. fusca* Kenaga, *T. indentata* Kenaga, *T. parva* Kenaga, *T. retusa* Kenaga, *T. ujhelyi* Esaki, *T. whitei* Bergroth.

Color pattern: Variegated yellow and black, predominantly yellow in some species. Head with longitudinal black stripes along eyes. Mesonotum with two longitudinal dark stripes on each side, with additional stripe mesad of them in some species.

Structures in wingless forms: Body oval. Male smaller and more slender than female. Pronotum in relation to mesonotum longer in male than in female. Head between eyes strongly widened posteriorly, posterior margin straight. Eye exserted, extending to nearly anterior half of pronotum. Antenniferous tubercles scarcely developed; antennal cavities open on or a little below straight line across anterior margins of eyes. Antenna over half as long as body, greater in absolute and relative length to body in male, but without significant difference in proportional lengths of segments between sexes. First segment strongly curved in basal half, much longer than second segment, but not over twice as long as the latter; second segment shortest, truncate at apex; third segment always over twice as long as second, slender, simple at apex; fourth segment about as thin as third, a little shorter than third. Clypeus with basal margin obliterated. Mandibular and maxillary plates indistinguishably fused. Rostrum relatively long and slender, reaching mesosternum; third segment three times as long as last segment.

Pronotum shorter and much narrower than head, anterior margin straight, posterior margin variable, lateral margin rounded. Mesonotum with median longitudinal sulcus obscure, recognizable posteriorly; over two and a half times as long as pronotum. Intersegmental suture between mesonotum and metanotum slightly produced anteromesially. Metanotum laterally defined by longitudinal elevation, median longitudinal sulcus normally recognizable throughout the entire length. Metasternum highly reduced, less than one tenth as long as mesosternum but a little longer than second ventrite, without either omphalium or omphalial groove. Front leg slender and relatively long; femur slightly longer than tibia; tibia simply thickened apically, without conspicuous process, inner surface with longitudinal shallow depression apically; tarsus with first segment highly reduced, second segment three to five times as long as first segment, claws arising from beyond middle and with membranous arolium. Middle leg with femur robust, much thicker than tibia, between two thirds and three fourths as long as tibia; tibia over three times as long as first tarsal segment; first tarsal segment longer than second tarsal segment, but not over one and a half times as long as second; second segment with poorly developed claws. Hind leg with femur a little less than twice to a little over twice as long as tibia; tibia over four times as long as first tarsal segment; first tarsal segment about as long as second tarsal segment, second segment with claws.

Abdomen has connexivum strongly reflexed, but not folded on dorsum in female. Anterior margins of first and second tergites convex, which are often obliterated medially, both segments much longer than any one segment that follows posteriorly.

Male: Seventh segment at least twice as long as sixth segment, concave on ventral apical margin. Eighth segment prolonged in some species, simply concave or notched at middle on ventral apical margin, ventral surface with a median longitudinal groove and densely clothed with hairs on either side of the groove (*indentata*), or depressed in some species. Ninth segment with suranal plate laterally hidden beneath eighth tergite; pygophore exposed at least apically; parameres simply curved upward, short but robust. Apical segment of endosoma with dorsal plate basally bifurcate, fused anteriorly with large apical plate which extends along ventral apical area of endosoma; lateral plates slender, reaching anteriorly near point of fusion or dorsal plate with apical plate, extending posteriorly beyond base of dorsal plate; without ventral plate. (Description of the genitalia is based on *whitei, indentata,* and *fusca.*)

Female: Seventh segment ventrally much longer than sixth segment, deeply concave on ventral apical margin. Eighth segment ventrally well exposed beyond concave ventral apical margin of seventh segment. First valvula with outer lobe simply narrowed apically, inner lobe membranous, folded beneath outer lobe but not reaching apex of outer lobe, a dark thread-like structure arising from near base and extending as far as apex of outer lobe. Second valvulae constricted near apices, extending far beyond apical margin of intervalvular membrane which is concave; process of ninth tergite robust. Vulva slender, reaching apical one fourth of first valvulae. (Description of the genitalia is based on *whitei.*)

Winged forms: Forewing with well formed hairy embolium, anterior branch from basal R + M + Cu is connected with embolium at its lower apical angle; posterior branch is connected with vein A before middle of hemelytron. In apical membranous region there are two veins, the anterior one from apex of embolium and lower one from the point of union between A and the posterior branch from R + M + Cu. The line of weakness represented by pale straight region spreading entire membranous region at middle, basal line of weakness is represented by fine thinly pigmented line behind basal coriaceous region. Hind wing with Cu evanescent apically. No vein A is recognized. Pronotum subpentagonal in shape, widest at a little behind middle, apex broadly rounded.

Distribution: Central and South America (Bolivia, Brazil, British Honduras, Costa Rica, Colombia, Mexico, Panama, Peru, Puerto Rico).

The genus *Telmatometra* is distinguishable from *Trepobates* by the following characteristics:

(1) Sexual difference in proportional lengths of the first and second antennal segments is absent.

(2) The male has relatively and absolutely longer antennae than the female.

(3) The length of the third rostral segment relative to the second is greater than in *Trepobates.*

(4) The length of the tibia in relation to the femur in the front leg is greater than in *Trepobates.*

(5) The first tarsal segment is about as long as second in the hind leg, while it is distinctly longer than second in *Trepobates.*

(6) The intersegmental suture between mosonotum and metanotum is produced anteromesially.

(7) There is evidence that the growth ratio for the third antennal segment is greater than those for the first and second segments in *Telmatometra.*

Genus *Trepobatoides* Hungerford and Matsuda

(Figs. 52, 125, 142, 169, 992-1002)

Trepobatoides Hungerford and Matsuda, Florida Ent., 41(3):125-128(1958).

Type species: *Trepobatoides boliviensis* Hungerford and Matsuda, by original designation.

Species examined: *T. boliviensis* Hungerford and Matsuda.

Color pattern: Predominantly pale yellow. Head with median black longitudinal stripe. Pronotum with a median black longitudinal stripe and a pair of black spots on either side of middle; mesonotum with a median black longitudinal stripe and a pair of lateral longitudinal stripes of the same color extending for entire length of mesonotum; mesopleural region with a black longitudinal stripe which extends back as far as metathoracic spiracle. Metanotum with a pair of large black spots along anterior margin. Each abdominal tergite with both anterior and posterior margins black.

Structures in wingless forms: Body elongate ovate, much narrowed anteriorly. Head between eyes longer than wide, widened posteriorly, posterior margin slightly produced posteriorly. Eye oblong, covering anterolateral angle of pronotum. Antennal cavities open just above anterior margins of eyes. Antenna slender, a little shorter than length of body. First segment distinctly longer than two following segments together; second segment shortest, its relative length to first segment greater in male than in female; third segment with apex truncate; fourth segment much longer than third segment. Clypeus with basal margin obliterated. Mandibular and maxillary plates completely fused. Rostrum long, extending far beyond prosternum; third segment about two and a half times as long as last segment.

Pronotum much narrower than head, posterior margin feebly concave, posterolateral angle broadly rounded. Mesonotum without distinct median longitudinal sulcus, its relative length to pronotum greater in male than in female. Intersegmental suture between mesonotum and metanotum feebly concave dorsally. Metanotum laterally defined by longitudinal elevations with a faint median longitudinal sulcus. Metasternum a little less than one tenth as long as mesosternum, without omphalium. Front leg considerably thicker and longer than tibia; tibia slightly thickened apically, without armature on inner apical angle in both sexes; tarsus a little less than half as long as tibia; first segment strongly reduced; second segment three times as long as first, claws arising from middle of inner margin, with hair like arolium, Middle leg with femur thick, about two thirds as long as tibia; tibia a little over three times as long as first tarsal segment; first tarsal segment a little less than twice as long as second tarsal segment; claws very small. Hind leg with femur about twice as long as tibia; tibia slightly thickened at base, then tapering apically, five to six times as long as first tarsal segment; first tarsal segment a little shorter than second segment, claws inconspicuous.

Abdomen oblong, a little narrower in male. Connexivum not strongly reflexed. First tergite with anterior margin roundly produced and distinct; second segment also produced on anterior margin; third to sixth tergites subequal in length in both sexes; second to sixth ventrites subequal in length in both sexes.

Male: Seventh segment ventrally over twice as long as sixth segment. Eighth segment strongly prolonged and cylindrical, ventrally about twice as long as seventh in the middle, roundly depressed along posterior margin. Ninth segment with suranal plate widened posteriorly; pygophore well exposed, nearly truncate on apical margin, densely clothed with adpressed hairs on ventral surface; parameres simply curved upward. Endosoma long. Dorsal plate thick and bifurcate basally, apically fused with apical plate via narrow bridge; without well defined lateral plates; broadly sclerotized along ventral margin of endosoma; without either ventral or basal plate.

Female: Seventh segment ventrally about three times as long as sixth segment, ventral apical margin broadly concave. Eighth segment ventrally well exposed. First valvula with inner lobe dark, with two apical processes, inner one of them shorter and attached to vulva, outer one almost reaching apex of outer lobe of first valvula. basally covering outer lobe beneath; with a tuft of straight long hairs on lower lateral margin of the dilated base of outer lobe. Second valvula directed mesad apically and broadly rounded apically; intervalvular membrane directly continuous with apices of valvulae, dark along outer margin; ramus slender and long, without crescent shaped sclerite at apex of process of ninth tergite.

Distribution: South America (Bolivia).

The genus *Trepobatoides* is related to *Telmatometra* and its allies but peculiar in the following characteristics:

(1) The head above has a black longitudinal stripe. This is true of *Trepobates* but not of *Telmatometra* (except for *rozeboomi*), *Halobatopsis, Cryptobates,* etc.

(2) The first antennal segment is much longer than the two following segments together. In no other genera of Trepobatinae is the first segment much longer than two following segments together.

(3) The length of the second antennal segment in relation to the first is greater in the male than in the female. In the related genus *Trepobates* the length of the second segment relative to the first is greater in the female than in the male.

(4) The female genitalia are peculiar in that: (1) The inner lobe of the first valvula covers the outer lobe beneath basally, and has a tuft of long hairs on the lateral margin of each side of outer lobe, and (2) the second valvulae are apically so approximated as to obliterate the apical margin of the intervalvular membrane.

(5) The relative lengths of the first and second tarsal segments of the middle leg are close to 2:1; while the same proportion never exceeds 1.5:1 in *Trepobates* and *Telmatometra.*

Although the relative lengths of the leg segments are more like those of *Telmatometra,* the relatively short rostrum suggests a relationship to *Trepobates.* The extremely long first antennal segment suggest a closer relationship to *Trepobates* than to *Telmatometra,* in which the first antennal segment is not the longest. The male genital segment is, however, similar to that of *Telmatometra acuta.* This genus thus represents an intermediate between *Trepobates* and *Telmatometra.* Different proportional lengths of antennal and leg segments from those in the related genera are apparently derived from different growth patterns from those in the related genera, considering the fact that the body length of this genus is about the same as in *Trepobates, Telmatometra,* etc.

Genus *Halobatopsis* Bianchi

(Figs. 50, 143, 163, 1003-1011, 1019-1025)

Halobatopsis Bianchi, Ann. Mus. Zool. St. Petersbourg for the year 1896, p. 70 (1896).
Halobatopsis Esaki, Ann. Mus. Nat. Hung., 23:136-138(1926).
Halobatopsis Drake and Harris, Iowa St. Coll. Jour. Sci., 15(3):237-240(1941).
Halobatopsis Kenaga, Jour. Kansas Ent. Soc., 15(4):136(1942).

Type species: *Halobates platensis* Berg, by original designation.

Species examined: *H. platensis* (Berg), *H. spiniventris* Drake and Harris.

Color pattern: Variegated black and pale yellow to pale brown.

Structures in wingless forms: Head between eyes strongly widened posteriorly, posterior margin feebly concave. Eye exserted, extending posteriorly as far as middle of pronotum. Antenniferous tubercles scarcely developed; antennal cavities open on or above line across anterior margins of eyes. Antenna over half as long as body, without sexual difference in relative lengths between segments, and in relative length of antenna to length of body. First segment slightly curved at base, twice or a little less than twice as long as second; second segment shortest; third segment less than one and a half times as long as second segment, apex truncate; fourth segment about as long as or longer than third segment. Clypeus with basal margin obliterated. Mandibular and maxillary plates indistinguishably fused. Rostrum with third segment relatively thick basally and about two and a half times as long as last segment.

Pronotum narrower than head including eyes, lateral margins broadly rounded, posterior margin concave at middle. Relative length of mesonotum to pronotum greater in female than in male. Mesosternum with posterior margin concave. Intersegmental suture between mesonotum and metanotum slightly produced anteriorly at middle. Metanotum laterally defined by longitudinal elevations, without median longitudinal sulcus. Metasternum highly reduced, less than one tenth as long as mesosternum, without omphalium, distinctly longer than second ventrite. Front leg with femur strongly arched in male of *spiniventris;* tibia distinctly shorter than femur, strongly curved, constricted beyond middle and with a dense row of short black hairs on inner surface; tarsus with first segment greatly reduced, second segment with claws arising from beyond middle of second segment. Middle leg with femur two thirds to three fourths as long as tibia; tibia a little less than three times as long as first tarsal segment; first tarsal segment less than one and a half times as long as second segment, second segment with poorly developed claws. Hind leg with femur about twice as long as tibia; tibia over four times as long as first tarsal segment; first tarsal segment subequal in length to second; second segment with claws longer than those in middle leg.

Abdomen with connexivum strongly reflexed but not folded on dorsum in female of *spiniventris*. Anterior margins of first and second tergites produced anteriorly, obliterated at middle, both segments much longer than any one of following segments.

Male: Seventh segment over two and a half times as long as sixth segment and concave on ventral apical margin. Eighth segment concave on ventral apical margin or with a median spinous process (*spiniventris*). Ninth segment with suranal plate simple; pygophore exposed in apical half, broadly rounded on apical margin; parameres robust. Endosoma with dorsal plate bifurcate basally, apically directed cephalad along ventral margin of endosoma (fused apical plate); without well defined lateral plates, sclerotized along ventral margin of endosoma; without either ventral or basal plate. Description of the genitalia is based on *spiniventris*.)

Female: Similar to Telmatometra. Seventh segment deeply concave on ventral apical margin. Eighth segment thus ventrally well exposed behind seventh ventrite. First valvula with inner lobe folded beneath outer lobe, split apically into two lobes and both nearly reaching apex of outer lobe, largely fused with vulva on inner margin. Second valvula far extending beyond apical margin of intervalvular membrane, folded upward and rounded apically, apical margin of intervalvular membrane concave and sclerotized; ramus very long. Vulva long, reaching near apex of first valvula. (Description of the genitalia is based on *spiniventris*.)

Winged forms: Hemelytra with well formed hairy embolium. R + M + Cu sends two branches, anterior one of them united with inner apical angle of embolium, then sending a branch into apical membranous region; the posterior branch united with A before middle of wing, then extending into membranous region. Line of weakness represented by a transverse weakly pigmented area, which stretches throughout the middle of the entire membranous region of wing. Hind wing with vein A obscure, connected with R + M beyond the cross vein connecting Sc and R + M. Pronotum subpentagonal, widest behind middle.

Distribution: South America (Argentina, Brazil, Uruguay.)

The genus *Halobatopsis* differs from *Telmatometra* by the following characteristics:

(1) There is no conspicuous sexual difference in proportional lengths of antennal segments or in the length of the antenna in relation to the total length of body in *Halobatopsis.*

(2) The third antennal segment is distinctly less than twice as long as the second, while it is distinctly over twice as long as the second in *Telmatometra.*

(3) The abdomen is predominantly black, while it is predominantly yellow in *Telmatometra.*

The genus *Halobatopsis* is also closely related to *Trepobates,* but can be distinguished from it by:

(1) The eyes extending beyond the middle of the pronotum in lateral view, while they do not extend beyond middle in *Trepobates.*

(2) The hind tibia is over twice as long as the tarsus, while it is distinctly less than twice as long as the tarsus in *Trepobates.*

(3) The abdomen is relatively wider in *Halobatopsis* than in *Trepobates.*

Genus *Ovatametra* Kenaga

(Figs. 55, 125, 143, 163, 1026-1036)

Ovatametra Kenaga, Jour. Kansas Ent. Soc., 15(4):136-137(1942).

Type species: *Halobatopsis peruvianus* Drake and Harris, by original designation.

Species examined: *O. fusca* Kenaga, *O. obesa* Kenaga, *O. minima* Kenaga, one unidentified species.

Color pattern: Variegated pale yellow to pale brown and black. Head with a pair of lateral and median black longitudinal stripes which are often confluent posteriorly. Pronotum with a pair of lateral black spots and a median black stripe. Mesonotal region typically with a pair of lateral and median longitudinal stripes; mesopleural region with two black longitudinal stripes. Metanotum and abdominal tergites largely black.

Structures in wingless forms: Oval. Female considerably longer and wider than male. Head between eyes widened posteriorly, posterior margin weakly concave. Eye exserted, extending posteriorly, covering a large part of lateral margin of pronotum. Antenniferous tubercles scarcely developed; antennal cavities open above line across anterior margins of eyes. Antenna slender, over half the length of body, without significant difference in proportional lengths of antennal segments between sexes. First segment distinctly longer than second segment, but shorter than two following segments together; second segment as long as or a little shorter than third segment; third segment with apex truncate; fourth segment longer than third. Clypeus with basal margin obliterated. Mandibular and maxillary plates indistinguishably fused. Rostrum with third segment less than twice as long as last segment.

Pronotum narrower than head including eyes, posterior margin roundly produced posteriorly in female, nearly straight in male of *minima*, lateral margin rounded. Relative length of mesonotum to pronotum greater in female than in male, without median longitudinal sulcus. Intersegmental suture between mesonotum and metanotum concave dorsally. Metanotum laterally defined by longitudinal carina, without median longitudinal sulcus. Metasternum highly reduced, without omphalium, less than one tenth as long as mesosternum. Front leg with femur distinctly longer than tibia; tibia over twice as long as tarsus; tarsus with first segment greatly reduced, claws arising from near middle. Middle leg with femur robust, about two thirds as long as tibia; tibia a little less than three times as long as first tarsal segment; first tarsal segment a little longer than second segment. Hind leg with femur twice or a little less than twice as long as tibia; tibia about two and a half times as long as first tarsal segment; first tarsal segment a little longer than second segment.

Abdomen with connexivum usually strongly reflexed. Anterior margins of first and second tergites roundly produced anteriorly but more or less obliterated at middle; both segments longer than any one following segment.

Male: Seventh segment with ventral apical margin concave and feebly notched at middle in *minima*, or simply concave and less than three times as long as sixth segment ventrally. Eighth segment with ventral surface strongly depressed and hairy in *minima*. Ninth segment telescoped within cavity formed by elongated eighth segment; suranal plate simple; pygophore apically exposed; parameres robust and simply curved upward. Endosoma with dorsal plate thickened at base, extending anteriorly along apical margin of endosoma (probably fused with apical plate); lateral plates two paired, one along dorsal plate, the other along ventral margin of endosoma; without well defined basal and ventral plates. (Description of the genitalia is based on *minima* and one unidentified species.)

Female: Seventh segment ventrally less than three times as long as sixth segment, its ventral apical margin broadly concave. First valvula with inner lobe well pigmented, folded beneath outer lobe, with basal thickening and apical thread like process; outer lobe simply narrowed apically, membranous and rounded apically. Second valvula with apex rounded and convergent from each side; apical margin of intervalvular membrane thus obliterated, with V-shaped, dark area on the membrane; ramus fine and long; process of ninth tergite wtih a crescent shaped sclerite at apex at the point of union with ramus of first valvula. Vulva membranous, slender, free from inner lobe of first valvula. (Description of the genitalia is based on *O. fusca* and one unidentified species.)

Distribution: South America (Bolivia, Brazil).

The genus *Ovatametra* is closely related to *Halobatopsis*, from which it can be separated by the following characteristics:

(1) The body is smaller in *Ovatametra* than in *Halobatopsis.*

(2) The head has a median black longitudinal stripe in *Ovatametra.*

(3) The endosoma is provided with two pairs of lateral plates in *Ovatametra*, while it is without well differentiated lateral plates in *Halobatopsis.*

(4) The third antennal segment is only slightly longer than or equal to the second in *Ovatametra*, while it is distinctly longer than the second segment in *Halobatopsis.*

(5) The third rostral segment is less than twice as long as the last segment in *Ovatametra*, while it is about two and a half times as long as the last segment in *Halobatopsis.*

(6) The middle tibia is not as long as the body in *Ovatametra*, while it is as long as the body in *Halobatopsis.*

(7) The hind femur is less than twice as long as the front femur in *Ovatametra*, while it is over twice as long as the front femur in *Halobatopsis.*

(8) The middle tarsus is subequal to or longer than the middle femur in *Ovatametra*, while the same is shorter than the middle femur in *Halobatopsis.*

The above-mentioned differences in proportional lengths may be attributable to similar allometric growth patterns for the segments, since *Ovatametra* is definitely shorter in body size than in *Halobatopsis.* The differences, therefore, need to be reinvestigated in terms of allometric changes.

Genus *Rheumatometroides* Hungerford and Matsuda

(Figs. 56, 1037-1049)

Rheumatometroides Hungerford and Matsuda, Pan-Pacific Ent. 34(4):203-206 (1958).

Type species: *Rheumatometroides browni* Hungerford and Matsuda, by original designation.

Species examined: *R. browni* Hungerford and Matsuda.

Color pattern: Predominantly black, with testaceous markings. Head with broad black median longitudinal stripe. Pronotum with testaceous spot at middle. Mesonotum with a large W-shaped testaceous marking. Mesopleuron and metapleuron with broad black bands, the former with a band of grayish pile superimposed. Thoracic venter pale testaceous; abdominal tergites predominantly black; venter more or less brown.

Structures in wingless forms: Head between eyes widened posteriorly, slightly dilated just in front of eyes, dorsal posterior margin of head straight. Eye covering anterolateral angle of pronotum, inner margin slightly sinuate. Antennal cavities placed much anterior to eyes. Antenna shorter than length of body; first segment longest, with spinous hairs sparsely scattered; second segment a little longer than third, second and third segments together longer than first; fourth segment a little longer than third. Clypeus with basal margin obliterated, laterally well defined. Mandibular and maxillary plates almost completely fused. Rostrum with first segment relatively long; third segment less than twice as long as last segment.

Pronotum narrower than head including eyes, posterior and lateral margins rounded. Mesonotum over twice as long as pronotum, with distinct median longitudinal sulcus, with medially keeled longitudinal groove extending throughout entire length of mesonotum in female, posterior margin concave and incised at middle. Intersegmental suture between mesonotum and metanotum anteromesially produced. Metasternum about one tenth as long as mesosternum. Metacetabular region convergent anteriorly in female. Metanotum without median longitudinal sulcus. Metasternum rather strongly produced anteriorly on basal margin in male; omphalium present, more distinct in male, located closer to anterior margin than to posterior margin of metasternum. Front leg slender, without sexual difference in shape; tibia simply thickened apically and flattened; first tarsal segment greatly reduced, second segment three and a half times as long as first segment, claws arising from near middle. Middle leg with femur robust and a little shorter than tibia; tibia a little over three times as long as first tarsal segment; first tarsal segment as long as second. Hind leg with femur about two and a half times as long as tibia; tibia about six times as long as first tarsal segment; first tarsal segment shorter than second tarsal segment, claws inconspicuous in both middle and hind legs.

Abdomen with connexivum strongly reflexed and folded on dorsum in both sexes. Anterior margin of first tergite distinct, roundly produced anteriorly, first tergite much longer than second tergite, anterior margin of succeeding segments well impressed and straight.

Male: Seventh ventrite greatly prolonged, over twice as long as sixth. Eighth segment broadly rounded on dorsal apical margin, nearly straight on ventral apical margin. Ninth segment with suranal plate provided with a pair of lateral long processes directed cephalad; pygophore with apical margin simply rounded; parameres reduced but distinctly recognizable. Endosoma with definitive dorsal plate extending to apical margin and turned backward, basally indistinguishably fused with basal plate, which in turn bears apically slender black sclerite apparently giving support to membranous ventral plate, as in *Trepobates.* (Description of the genitalia is based on *browni.*)

Female: Seventh ventrite over twice as long as sixth, produced posteriorly at middle. Eighth segment with first valvula simply narrowed apically, apex membranous; inner lobe not distinct from outer lobe, attached largely to vulva, apex of outer lobe membranous, membranous lobe arising from near base and directed laterally; ramus attached to the apex of process of ninth tergite. Second valvula simply narrowed apically, serrulate on outer margin apically; intervalvular membrane produced, reaching near apices of second valvulae; ramus slender, extending back beyond middle of second valvulae and rounded at apex; process of ninth tergite sclerotized, simply narrowed at apex. Vulva with apex rounded, thinly sclerotized, reaching middle of first valvulae. (Description of the genitalia is based on *browni.*)

Distribution: The Solomon Islands.

The genus *Rheumatometroides* is quite peculiar in the following characteristics:

(1) The first rostral segment is long.

(2) In the female the mesonotum is provided with a distinct medially keeled longitudinal groove.

(3) The omphalium is present.

(4) The suranal plate in the male is provided with a conspicuous lateral process.

In the female of *Rheumatometra philarete* Kirkaldy the mesonotum also has a median longitudinal groove, but only posteriorly. In *Hynesionella* and *Metrobatopsis* the suranal plate also has conspicuous process on each side, but these have probably developed independently in these genera. The omphalium occurs in this species and *Stenobates*. As mentioned elsewhere this genus is closely related to *Stenobates*.

Genus *Stenobates* Esaki

(Figs. 58, 1050-1057)

Stenobates Esaki, Entomologist, 60(771):181(1927).
Stenometra Esaki, Ann. Mus. Nat. Hung., 23:119-120(1926) (preoccupied, type species, *Stenometra biroi* Esaki).

Type species: *Stenometra biroi* Esaki, by original designation.

Species examined: *S. biroi* (Esaki).

Color pattern: Head with three longitudinal dark stripes on yellow ground color. Pronotum with a pair of yellow round spots along anterior margin, the rest black. Mesonotum with two pairs of pale yellow longitudinal stripes on black ground color. Abdomen above black. Body beneath, rostrum and legs predominantly yellow.

Structures in wingless forms: Head longer than wide at base between eyes, posterior margin straight. Eye covering anterolateral angle of pronotum. Antennal cavities located far beyond anterior margins of eyes. Antenna slender, shorter than body. First segment simple, longer than two following segments together; second and third segments simple; second segment longer than third; fourth segment about as long as third. Clypeus widened anteriorly, basal margin obliterated. Mandibular and maxillary plates almost completely fused. Rostrum very thick, first segment relatively long; third segment concave on upper margin, strongly thickened basally on lower margin, less than twice as long as last segment.

Pronotum shorter than head, posterior margin broadly rounded. Mesothorax gently widened posteriorly, median longitudinal sulcus (groove) distinct posteriorly in male. Intersegmental suture between mesonotum and metanotum produced anteromesially. Metanotum without median longitudinal sulcus. Metacetabular regions well elevated and defined from metanotal region, convergent anteriorly. Metasternum angularly produced anteriorly, much longer than second abdominal ventrite, about one fourth as long as mesosternum in male; *highly conspicuous omphalium located at intersegmental suture between mesosternum and metasternum.* Front leg with femur slender; tibia strongly widened apically, flattened and thin; tarsus a little shorter than tibia, first segment highly reduced; second segment about six times as long as first, slender claws and membranous arolium arising from near middle. Middle leg slender; femur five sixths as long as tibia, relatively long and slender; tibia about three times as long as first tarsal segment; tarsus with first segment a little longer than second. Hind leg much shorter than middle leg. Femur about three times as long as tibia; tibia over five times as long as first tarsal segment; first tarsal segment a little shorter than second.

Abdomen in male: Connexivum reflexed on dorsum. First tergite with anterior margin distinct and roundly produced anteriorly; second and third tergites with anterior margins distinct; ventrites not highly reduced. Seventh ventrite longer than two precedings together. Eighth tergite well developed and broadly rounded on apical margin. Ninth segment with suranal plate having conspicuous process on each side; pygophore small, rounded on apical margin.

Female: Female specimen was not available for study.

Distribution: The Oriental region (Singapore).

The genus *Stenobates,* which is known only from the type species, is apparently closely related to *Rheumatometroides* as is evidenced by the following characteristics which they share in common:

(1) The relative lengths of leg segments are very similar.

(2) The intersegmental suture between the mesonotum and metanotum is produced anteriorly at the middle.

(3) The dorsal posterior margin of the head is straight.

(4) The thick and reflexed rostrum.

(5) The elevated metacetabular regions are convergent anteriorly.

(6) The omphalium is retained.

(7) The suranal plate is provided with a spinous process on each lateral margin.

(8) The front tibia is strongly flattened, and simply but strongly widened apically.

The genus *Stenobates*, however, can easily be separated from *Rheumatometroides* by the quite distinct shape of the front tibia in the male and the omphalium being much more conspicuous and located at the anterior limit of the metasternum where it is strongly produced anteriorly.

Genus *Cryptobates* Esaki

(Figs. 51, 1058-1071)

Cryptobates Esaki, Ann. Mag. Nat. Hist. 10(4):412-415(1929).
Cryptobates Hungerford and Matsuda, Jour. Kansas Ent. Soc., 31(4):246-248 (1958).

Type species: *Gerris raja* Distant, by original designation.

Species examined: *C. kuiterti* Hungerford and Matsuda, *C. raja* (Distant).

Color pattern: Pale yellow in ground color, black along inner margins of eyes; pronotum with either a broad single or paired black median longitudinal stripes, and paired lateral stripes of the same color; mesonotum with three black longitudinal stripes; abdominal tergites variable in color, first tergite with a transverse yellow spot on each side. Hemelytra dark fuscous.

Structures in wingless forms: Head between eyes a little longer than wide, widened posteriorly, posterior margin straight. Eye exserted, inner margin slightly rounded, covering anterolateral angle of pronotum. Antennal cavities open just above anterior margins of eyes. Antenna slender and about as long as body in female (not known for male). First antennal segment much longer than second but shorter than third or fourth, incrassate apically; second segment shortest and more slender than first, apex thick and truncate; third segment much more slender than second, over twice as long as second; fourth segment as thin as third, as long as or just a little shorter than third, clothed with hairs which are considerably longer than those on third. Clypeus with basal margin faint but recognizable. Mandibular and maxillary plates recognizable by faint suture separating them. Rostrum very long, reaching near middle of mesosternum; first segment about half as long as head on ventral surface; third segment three times as long as last segment.

Pronotum a little narrower than head including eyes; lateral margins divergent posteriorly, posterior margin broadly rounded and produced posteriorly or feebly bisinuate, mesonotum convex, about two to three times as long as pronotum. Mesosternum convex, posterior margin concave. Intersegmental suture between mesonotum and metanotum nearly straight dorsally. Metanotum declivent posteriorly, completely fused with first abdominal tergite, without median longitudinal sulcus, laterally defined by strongly elevated area. Metasternum greatly reduced, a little less than one twentieth as long as mesosternum, omphalium absent. Front leg slender and long, a little shorter than total length of body. Femur slender, about the same in thickness throughout, a little longer than tibia; tibia simply thickened apically, inner apical angle without conspicuous process in both sexes; tarsus with first segment greatly reduced, but relatively longer than in other genera of the subfamily; second tarsal segment three and a half times as long as first segment, claws arising from apical third of inner margin of second segment. Middle leg with femur thick, slightly narrowed beyond middle, a little shorter than tibia; tibia about three times as long as first tarsal segment; first tarsal segment less than one and two thirds times as long as second segment; second tarsal segment slightly curved apically, claws very inconspicuous. Hind leg with femur two to two and one half times as long as tibia; tibia about three to four times as long as first tarsal segment; first tarsal segment as long as or a little shorter than second tarsal segment, second segment has claws rather inconspicuous.

Abdomen strongly declivent posteriorly. Connexivum nearly vertically erected. Anterior margins of first and second tergites obliterated, anterior margin of third tergite straight and distinct.

Male: Seventh segment ventrally a little shorter than five preceding ventrites together. Eighth segment greatly prolonged, its ventral apical margin feebly bisinuate. Ninth segment with suranal plate long, widened in apical two thirds; pygophore ventrally well exposed, its apical margin feebly notched at middle; parameres greatly developed. Endosoma with dorsal plate extending as far as apical margin of endosoma, separated from apically bifurcate apical plate in *kuiterti,* basally extending along basal margin of endosoma; ventral plate membranous or short but sclerotized in *kuiterti,* basally detached from dorsal (or dorsal plus basal) plate; lateral plates long and oblique; apex of endosoma sclerotized and slightly produced. (Description of the genitalia is based on *raja* and *kuiterti.*)

Female: Seventh segment a little shorter than five preceding segments together ventrally, ventral apical margin concave. Eighth segment well exposed ventrally. First valvula with inner lobe well pigmented, forked into two slender processes, one of them reaching near apex of outer lobe; outer lobe simply narrowed apically, apex acute; ramus reaching basal region of outer margin of the process of ninth tergite. Second valvula well pigmented on outer margin, apex broadly rounded and directed mesad or simply rounded apically, extending far beyond apical margin of intervalvular membrane. Vulva membranous and slender, largely free from inner lobe of first valvula. (Description of the genitalia is based on *kuiterti.*)

Winged forms: Hemelytra with basal coriaceous region occupies about basal two fifths, with broad embolium; two apical veins in membranous region, anterior one coming from lower (posterior) apical angle of embolium, the posterior one from the point of union of R + M + Cu and A. Line of weakness white and distinct, along apical margin of basal coriaceous region and horizontally on middle of hemelytron.

Distribution: The Oriental region (Burma, Southern India).

The genus *Cryptobates* appears to be related to *Telmatometra* in having a long rostrum, the first antennal segment not being the longest, the long front legs, etc., but can be distinguished from it by the following characteristics:

(1) The middle tibia is only slightly longer than the middle femur.

(2) The anterior margins of the first and second abdominal tergites are completely lost.

(3) The basal margin of the clypeus and the suture separating the mandibular and maxillary plates are recognizable.

(4) The metanotum is without median longitudinal sulcus.

Esaki (1929) believed that this genus is most closely related to *Amemboa,* but *Amemboa* actually belongs to the other subfamily, Gerrinae.

Genus *Naboandelus* Distant

(Figs. 61, 1072-1080)

Naboandelus Distant, Ann. Mag. Nat. Hist., 8(5):151(1910).
Naboandelus Distant, Faun. Brit. Ind., Rhynch., 5:163-164(1910).
Naboandelus Brown, Brit. Mus. Exp. S. W. Arabia in 1937-1938, 1(16-19): 227-229(1951).

Type species: *Naboandelus signatus* Distant, monobasic.

Species examined: *N. bergevini* Bergroth, *N. signatus* Distant, and two unidentified species.

Color pattern: Predominantly black. Head with a large black spot surrounded by yellow to yellowish brown area on dorsal surface. Pronotum with a median yellow spot. Legs predominantly yellow or brown.

Structures in wingless forms: Head between eyes slightly widened posteriorly, posterior margin nearly straight or feebly convex. Eye semicircular in shape, posteriorly covering anterolateral angle of pronotum. Antennal cavities placed just above anterior margins of eyes. Antenna with first segment slightly curved at base, longest but distinctly shorter than second and third segments together; second segment a little longer than third; third segment shortest; fourth segment fusiform. Clypeus well elevated, basal margin distinct. Mandibular and maxillary plates fused. Rostrum moderately thick; third segment less than twice as long as last segment.

Pronotum shorter and narrower than head, posterior margin broadly rounded or nearly straight, lateral margin rounded. Mesonotum without median longitudinal sulcus. Mesosternum with apical margin concave. Intersegmental suture between mesonotum and metanotum feebly anteromesially produced. Metanotum without median longitudinal sulcus, laterally defined by longitudinal elevation. Metasternum about one seventh as long as mesosternum in *bergevini.* Front leg with femur slender, about one and one third as long as tibia; tibia simply thickened apically and without conspicuous apical process in female; tarsus with first segment highly reduced; second segment three to four times as long as first segment, claws arising from a little beyond middle, with hair like arolium. Middle leg with femur thick, about two thirds to three quarters as long as tibia; tibia two and a half to three times as long as first tarsal segment; first tarsal segment less than one and a half times as long as second segment; second segment with claws inconspicuous. Hind leg with femur a little less than two and a half times as long as tibia; tibia about five times as long as first tarsal segment; first tarsal segment much shorter than second; second tarsal segment with claws slender and not conspicuous.

Abdomen in female: Rather strongly declivent posteriorly on dorsal surface. Connexivum reflexed, more strongly so from fourth segment on posteriorly and ventral surface more or less exposed dorsally. First tergite with anterior margin indicated only by lateral pits, completely lost medially in *bergevini;* second tergite rather strongly roundly produced anteriorly at middle, third to seventh tergites subequal in lengths; second ventral segment less than half as long as metasternum; seventh ventrite twice as long as sixth ventrite, its posterior margin feebly concave; posterior tergites reflexed upward, thus eighth segment subvertically exposed behind seventh segment. Genitalia similar to those in *Rheumatometra* and *Hynesionella.* First valvula with inner lobe darker, broad at base, reaching apical region of outer lobe; ramus well pigmented, extending basally along outer margin of process of ninth tergite, apex of the process with a crescent shaped sclerite. Second valvula well pigmented except for apical region, which is rounded and slightly extending beyond apical margin of intervalvular membrane; ramus of second valvula slender. Vulva membranous, acutely pointed at middle and at each side. (Description of the female genitalia is based on *bergevini.*)

Winged forms: Hemelytra long and slender, far extending beyond tip of abdomen. Coriaceous region occupies basal one third of wing; venation as in other genera of Trepobatinae, R + M + Cu branches into two oblique veins more proximally than in other genera; line of weakness not quite reaching basal coriaceous region, narrow. Pronotum widest behind middle, broadly rounded on posterior margin.

Distribution: Oriental and Ethiopian regions (Angola, Arabia, Belgian Congo, Cameroons, Egypt, India, Madagascar, Somalia).

Although the phylogenetic position of this genus is not clear because of the absence of the male specimens available for study, this genus is probably close to *Hynesionella* from Africa. A close relationship to *Hynesionella* is indicated by:

(1) The similiar general color pattern.

(2) The rather strongly reflexed connexivum in the posterior abdominal segments in the female.

(3) The similar proportional lengths of the leg segments except for those in the distal middle leg segments.

(4) The similar proportional lengths of the antennal segments.

Genus *Hynesionella* Poisson

(Figs. 54, 1081-1092)

Hynesionella Poisson, Bull. Soc. Ent., France, 6:83(1949).
Hynesionella Hungerford and Matsuda, Jour. Kansas Ent. Soc., 32(1):37-41 (1959).

Type species: *Hynesionella aethiopica* Poisson, by original designation.

Species examined: *H. aethiopica* Poisson, *H. omer-cooperi* Hungerford and Matsuda.

Color pattern: Predominantly grayish black, with bluish tinge. Head with a large black spot, reddish brown along eyes and posterior margin of head. Pronotum with a median pale yellow spot.

Structures in wingless forms: Female much larger than male. Oval and robust. Head between eyes slightly widened posteriorly, basal margin feebly concave or nearly straight. Eye with inner margin emarginated in posterior half, covering anterolateral angle of pronotum. Antenniferous tubercles feebly developed; antennal cavities open on line across anterior margins of eyes. Antenna with first segment longest, slightly curved, shorter than two following segments together; second segment longer than third segment; third segment with apex truncate; fourth segment subequal to or a little longer than third. Clypeus short, basal margin recognizable. Mandibular and maxillary plates fused. Rostrum extending beyond prosternum; third segment about twice as long as last segment.

Pronotum with posterior margin produced posteriorly in the middle, lateral margins divergent anteriorly. Mesonotum widely and evenly depressed on median longiudinal axis; mesopleural region above coxa slightly narrowed; mesosternum with posterior margin concave, surface smooth and slightly convex. Intersegmental suture between mesonotum and metanotum well raised and carinate, produced posteriorly at middle in *omer-cooperi.* Metanotum without median longitudinal sulcus, short at middle, laterally defined by strong elevation reaching intersegmental suture between mesonotum and metanotum; metacetabular region rounded on lateral margin and convergent posteriorly. Metasternum much more reduced in length than in most other genera, a little longer than second ventrite. Front leg with femur thick near base, then narrowed apically, inner surface depressed and densely clothed with gray pubescence in *omer-cooperi,* incised near base on inner margin in male of *aethiopica;* tibia with inner apical angle more produced in male than in female. Middle leg with femur thick, about two thirds as long as tibia; tibia a little over twice to about three times as long as first tarsal segment; first tarsal segment a little over twice as long (?) or about as long as second segment; claws arising from near tip of second segment, inconspicuous. Hind leg with tibia half or a little less than half as long as femur, over seven times as long as first tarsal segment; first tarsal segment less than half as long as second segment; claws arising from beyond middle of second segment, slender and relatively long.

Abdomen strongly narrowed posteriorly in anterior half. Connexivum strongly reflexed. First tergite roundly produced on anterior margin, obliterated medially in male of *omer-cooperi;* second segment produced anteromesially, third to sixth tergites subequal in length. Ventrites more reduced.

Male: Seventh segment ventrally about half as long as second to fifth segments together. Eighth segment enormously developed ventrally, a little longer than all preceding segments together ventrally, about as long as third to seventh segments together dorsally, posterior half narrowed and narrowly rounded on apical margin dorsally; ventral surface with yellowish elevation laterally, slightly raised along median longitudinal axis. Ninth segment with lateral process of suranal plate conspicuous; pygophore exposed apically, apical margin broadly rounded; parameres highly vestigial. Endosoma with definitive dorsal plate extending along both apical and basal margins, bifurcate on both apices; lateral plates located beneath the base of dorsal plate, robust; ventral plate short and membranous, supported basally by slender oblique sclerite arising from near basal end of dorsal plate. Endosoma not prolonged apically. Proximal segment of endosoma sclerotized and lobate apically. (Description of the genitalia is based on *omer-cooperi.*)

Female: Seventh segment ventrally about twice as long as sixth segment; ventral apical margin simply concave. Eighth segment ventrally exposed. First valvula with inner lobe slender, folded beneath outer lobe, well sclerotized except for apical membranous region, reaching near apex of outer lobe, another shorter membranous lobe arising more cephalad; outer lobe greatly narrowed apically, sclerotized in outer half, a membranous lobe arising from base of outer lobe; ramus darkly pigmented, extending posteriorly along entire outer margin of process of ninth tergite, which is highly membranous and with sclerotized apical crescent shaped sclerite. Second valvula dark except for apical region, which is membranous, roundly folded and approximated to each other beyond apical margin of intervalvular membrane, which is dark and feebly notched at middle; ramus dark and slender. (Description of the genitalia is based on *H. omer-cooperi.*)

Distribution: Africa (East Cape Province, Ethiopia).

The genus *Hynesionella* is unique in the carinate, posteromesially produced definitive intersegmental suture between the mesonotum and metanotum.

Genus *Metrobates* Uhler

(Figs. 57, 126, 144, 164, 1093-1108)

Metrobates Uhler, Proc. Bost. Soc. Nat. Hist., 14:108(1871).
Metrobates Kirkaldy, Trans. Amer. Ent. Soc., 32:155(1906).
Metrobates Torre-Bueno, Trans. Amer. Ent. Soc., 37:246-249(1911).
Metrobates Anderson, Univ. Kansas Sci. Bull., 20(16):297-311(1932).
Metrobates Drake and Harris, Ann. Carnegie Mus., 21:83-88(1932).
Metrobates Deay and Gould, Amer. Midl. Nat., 17(4):764(1936).
Metrobates Drake and Harris, Ent. News, 56(10):284(1945).
Trepobatopsis Champion, Biol. Centr. Amer., Rhynch., 2:157(1898) (type species, *Trepobatopsis denticornis* Champion).

Type species: *Metrobates hesperius* Uhler, monobasic.

Species examined: *M. trux* (Bueno), *M. artus* Anderson, *M. denticornis* (Champion), *M. fugientis* Drake and Haris, *M. hesperius* Uhler, *M. plaumanni* Hungerford, *M. porcus* Anderson, *M. trux* (Bueno), *M. tumidus* Anderson.

Color pattern: Variegated grayish blue and black dorsally in most species. Grayish region entirely replaced by black in some species. Head always with reddish brown area at base. Pronotum with a median paler spot.

Structures in wingless forms: More or less strongly dorsoventrally flattened. Female much wider than male, without conspicuous sexual difference in length of body. Head between eyes strongly widened posteriorly, posterior margin nearly straight. Eye exserted, covering anterolateral angle of pronotum. Antenniferous tubercles scarcely developed; antennal cavities placed anterior to anterior margins of eyes. Antenna over half the length of body, without difference in proportional lengths of segments between sexes. First segment longer than three following segments together in some species, at least longer than two following segments together, strongly curved at base, thickened at middle, apex truncate, inner margin sparsely clothed with straight hairs in males, simply gradually thickened apically in females; second and third segments slightly curved and thickened apically, with comb shaped mass of short and thick hairs on inner distal angles of both segments more or less pronounced in most species, third segment always shorter than second; fourth segment a little longer than third in all species except *Plaumanni.* Clypeus with basal margin obliterated. Mandibular and maxillary plates, though clothed with hairs, recognizable from each other, and the latter smaller than former. Rostrum rather short, clothed with long hairs; third segment about twice as long as last segment.

Pronotum narrower than head including eyes, posterior margin variable, concave or convex, lateral margins broadly rounded.

Mesonotum with a faint median longitudinal sulcus throughout entire length. Mesosternum with a median longitudinal impression in most species, with a pair of tuberculous processes on posterolateral angles near base of mesocoxae in male of *porcus.* Intersegmental suture between mesonotum and metanotum more or less anteromesially produced. Metanotum without distinct median longitudinal sulcus, laterally defined by longitudinal elevations reaching the intersegmental suture. Metasternum over one tenth as long as mesosternum, without omphalium. Front leg with femur much longer than tibia, with a tubercle at middle of inner margin in male of *denticornis;* tibia with inner apical angle somewhat produced in male, longitudinally depressed near apex on inner margin; tarsus with first segment greatly reduced; second segment with claws arising from near middle on inner margin and with arolium. Middle leg with femur half to two thirds as long as tibia, thick and straight; tibia considerably longer than body, about seven times as long as first tarsal segment in most species; first tarsal segment much shorter than second segment, about one third as long as second in most species; second segment with claws arising from near apex of the segment and inconspicuous. Hind leg with femur over two and a half times as long as tibia; tibia two and a half times to three times as long as tarsus, and over ten times as long as first tarsal segment; first tarsal segment much shorter than second; second segment with claws arising from near middle and well developed.

Abdomen with connexivum not strongly reflexed. First and second tergites with their anterior margins distinct, both segments long. Ventrites considerably shorter than tergites.

Male: Seventh segment ventrally much longer than sixth segment, but never much over three times as long as sixth, ventral apical margin concave, nearly straight or feebly concave dorsally. Eighth segment cylindrical, strongly developed and with round apical margin dorsally, simply concave ventrally. Ninth segment with suranal plate exposed in apical half and with round apical margin; pygophore rounded on apical margin; parameres vary in shape and degree of development, conspicuous in most species and exposed on either side of pygophore. Endosoma with definitive dorsal plate extending along entire dorsal margin of endosoma, bifurcate on both ends; large apical plate (?) not connected with apex of dorsal plate; without either well defined lateral or ventral plate. (Description of the genitalia is based on *hesperius.*)

Female: Seventh segment about twice as long as sixth segment ventrally in most species, simply concave on ventral apical margin. Eighth segment ventrally well exposed. First valvula with inner lobe well sclerotized, folded beneath outer lobe, with two long apical processes, basally fused with vulva; outer lobe simply narrowed apically. Second valvula with apex directed somewhat mesad, rounded and membranous, considerably extending beyond apical margin of intervalvular membrane, where is well pigmented; ramus slender and long. Vulva largely membranous, medially produced on apical margin. (Description of the genitalia is based on *hesperius.*)

Winged forms: Hemelytra with basal coriaceous region occupying basal half of hemelytron, with broad embolium. Anterior apical vein arising from apex of embolium, lower (posterior) apical vein arising from point of union of vein A and R + M + Cu. Line of weakness broad. Pronotum in apical half broadly rounded, with a round pale spot near anterior margin at middle.

Distribution: Greater portion of the United States, Central and South America (British Honduras, Cuba, Guatemala, Haiti, Jamaica, Mexico, Peru, Puerto Rico, Venezuela).

The genus *Metrobates* is quite distinct from all other genera of the subfamily by the following characteristics:

(1) The strongly flattened body.

(2) The second and third antennal segments being conspicuously modified apically.

(3) The relatively long middle tibia.

(4) The conspicuous claws in the hind and middle legs and the long second tarsal segment bearing them.

(5) The presence of the median longitudinal impression on the mesosternum.

Genus *Rheumatometra* Kirkaldy

(Figs. 62, 63, 1110-1121, 1135-1141)

Rheumatometra Kirkaldy, Entomologist, 35:281(1902).
Rheumatometra Esaki, Ann. Mus. Nat. Hung., 23:144(1926).

Type species: *Rheumatometra philarete* Kirkaldy, monobasic.

Species examined: *R. philarete* Kirkaldy.

Color pattern: Head behind clypeus and along posterior margin with a yellow transverse band; the rest black on dorsal surface. Antennae black except for base of first segment yellow. Pronotum has a median longitudinal yellow stripe or spot. Mesonotal region with a longitudinal yellow stripe at middle in posterior half, the rest black with sublateral paler area on either side of middle. Mesopleural region with a yellow longitudinal stripe. Meso- and metacetabular regions above coxae yellow. Connexivum yellow to dark brown. Metanotum and tergites with grayish blue tinge. Body beneath pale reddish brown. Forewing dark reddish brown.

Structures in wingless forms: Female much larger than male. Head between eyes wide, wider at base than long at middle, posterior margin concave on either side of middle. Eye covering anterolateral angle of pronotum posteriorly. Antenniferous tubercles feebly developed; antennal cavities open on horizontal line across anterior margins of eyes. Antenna much shorter than body. First segment a little longer than second in male or much longer than second in female; second and third segments unmodified apically; second segment slightly longer than third; third segment a little shorter than fourth. Clypeus with basal margin distinct. Mandibular and maxillary plates distinct from each other. Rostrum rather thick; third segment about twice or less than twice as long as last segment.

Pronotum transverse, much shorter than head, about four times as wide as long at middle, posterior margin feebly produced posteriorly. Mesonotum with median longitudinal sulcus distinct and depressed towards intersegmental suture in posterior two thirds in female, without a distinct median longitudinal sulcus in male. Intersegmental suture between mesonotum and metanotum anteromesially produced. Mesothorax strongly widened posteriorly, more so in female. Mesopleural region with an oblique laevigate depression above mesocoxa outside mesoacetabular cleft. Metanotum without median longitudinal sulcus, defined laterally by elevated metacetabular region. Metasternum much longer than second ventrite, without either omphalium or omphalial groove, less than one sixth as long as mesosternum in female. Front leg with femur long and strongly arched in male; tibia also arched in male; both femur and tibia in female simple and the latter is shorter than former and without conspicuous apical thickening; first tarsal segment greatly reduced; claws arising from beyond middle of second tarsal segment. Middle leg with femur thicker in basal half, about two thirds as long as tibia, relatively shorter in male than in female; tibia a little less than twice as long as first tarsal segment, much thinner than femur; first tarsal segment over twice as long as second tarsal segment, relatively longer in female than in male. Hind leg with femur over twice as long as tibia in male, or less than twice as long as tibia in female; tibia about twice as long as tarsus in male; first and second tarsal segments fused.

Abdomen more strongly narrowed in male than in female. Connexivum not folded on tergum. First abdominal tergite with anterior margin obliterated medially; second tergite with anterior margin roundly produced at middle; third to sixth tergites and second to sixth ventrites subequal in length to each other.

Male: Seventh segment a little less than twice as long as sixth segment both dorsally and ventrally. Eighth segment with posterior margin simply concave ventrally, slightly concave on dorsal apical margin. Ninth segment largely telescoped within cavity formed by eighth segment. Suranal plate simple; pygophore small and simply rounded on apical margin; parameres rather small, arising from deep inside pygophore and exposed only apically. Endosoma with dorsal plate bifurcate basally, thickened apically and extends along apical margin of endosoma (probably fused part of apical plate); lateral plates slender and simple; without either basal or ventral plate. Basal segment of endosoma apically produced and sclerotized.

Female: Seventh segment a little less than twice as long as sixth segment ventrally; ventral apical margin simply concave. Eighth segment ventrally well exposed. *Genitalia much like those of Metrobates.* First valvula with inner lobe folded beneath outer lobe, well pigmented, branched into two apically, of which inner branch longer and extending to about middle of outer lobe; outer lobe narrowly pigmented along inner margin, apex membranous; ramus slender, attached to outer apical angle of well pigmented process of ninth tergite. Second valvula simply rounded apically, slightly extending beyond apical margin of intervalvular membrane, which is pigmented and notched at middle; ramus slender. Vulva simply rounded on apical margin, membranous basally and free from inner lobes of first valvulae.

Winged forms: Forewing with basal third of upper margin coriaceous, forming embolium. R + M + Cu forks into two apical branches at basal one fourth of wing; anterior branch goes obliquely to be united with inner apical angle of embolium, then sending further a branch into membranous region; posterior branch united with vein A, sending a vein apically. Line of weakness in membranous region evanescent basally. Hind wing much shorter than forewing. Pronotum relatively short, posterior half broadly rounded.

Distribution: Australia.

The genus *Rheumatometra* resembles *Metrobates* from the Western Hemisphere by the following similar characteristics:

(1) The similar general shape of the body and color pattern.

(2) The head is wide and the dorsal posterior margin is produced posteriorly.

(3) The clypeus with the basal margin well defined.

(4) The similar female genitalia.

(5) The presence of a median longitudinal sulcus on the mesonotum.

(6) The relatively long metasternum.

The genus, however, can easily be separated from *Metrobates* by the following characteristics:

(1) The quite distinct proportional lengths of antennal segments, and the absence of the distal comb on the second and third segments.

(2) The first and second tarsal segments are fused.

(3) The hind legs have the claws not conspicuous.

(4) The female is much larger than the male.

(5) The front leg of the male is greatly arched.

(6) The shorter pronotum.

(7) Quite distinct proportional lengths of leg segments.

(8) The absence of the median longitudinal impression on the mesosternum.

Genus *Metrobatopsis* Esaki

(Figs. 53, 1122-1134, 1142-1144)

Metrobatopsis Esaki, Ann. Mus. Nat. Hung., 23:144-146(1926).
Metrobatopsis Hungerford and Matsuda, Bull. Brooklyn Ent. Soc., 14(2):29-36 (1959).

Type species: *Metrobatopsis flavonotatus* Esaki, by original designation.

Species examined: *M. affinis* Esaki, *M. flavonotatus* Esaki, E. *solomonensis* Hungerford and Matsuda, two unidentified species.

Color pattern: Predominantly black. Pronotum always with a broad pale yellow spot at middle. Mesonotum with a single or a pair of round yellow spots.

Structures in wingless forms: Body oval, male much narrower than female. Head between eyes a little longer than wide, feebly widened at base, dorsal posterior margin nearly straight or feebly produced posteriorly. Eye exserted, covering anterolateral margin of pronotum. Antennal cavities open anterior to anterior margins of eyes. Antenna with first segment curved at base, more or less strongly incrassate in males of some species, longer than second; second segment always longer than third; third segment subequal to fourth segment; fourth segment fusiform and flattened. Clypeus elevated, basal margin distinct. Mandibular and maxillary plates fused. Rostrum extending beyond prosternum; third segment over twice as long as last segment.

Pronotum much narrower than head including eyes, posterior margin broadly rounded, lateral margins rounded, convergent anteriorly. Mesonotum depressed in posterior half at middle, without median longitudinal sulcus. Mesosternum simple, posterior margin concave. Intersegmental suture between mesonotum and metanotum anteromesially produced. Metanotum without median longitudinal sulcus, laterally defined by subparallel longitudinal elevation. Metasternum about one tenth as long as mesosternum in female, more strongly reduced in male, without either omphalium or omphalial groove. Front leg with femur considerably longer and thicker than tibia, thickest and strongly curved near base; tibia simply incrassate apically; tarsus with first segment greatly reduced, second segment three to four times as long as first segment, claws arising from beyond middle of second segment and with membranous arolium. Middle leg longer than hind leg; femur thick, subequal in thickness throughout, a little over two thirds as long as tibia; tibia slightly incrassate basally and tapering apically, about twice as long as first tarsal segment; first tarsal segment about twice to a little less than three times as long as second segment; second segment curved, slightly thickened at apex, claws small and inconspicuous. Hind leg with femur longer than middle femur, two and one fourth to three times as long as tibia; tibia about three times as long as tarsus; first and second tarsal segments fused.

Abdomen with connexivum strongly reflexed for all segments. Anterior margin of first tergite obliterated medially, that of second segment broadly roundly produced anteriorly, second tergite much longer than third tergite. Ventrites strongly reduced.

Male: Seventh segment greatly prolonged. Eighth segment greatly prolonged except for *M. affinis,* cylindrical. Ninth segment with suranal plate with a slender process on lateral margin near apex (except possibly for *affinis*); pygophore vertically rotated anteriorly except for *affinis,* with a median spinous process on median longitudinal axis except for *affinis;* parameres absent. Endosoma long, curved upward apically; apical segment of endosoma tightly ensheathed within heavily sclerotized basal segment of endosoma, definitive dorsal plate small, bifurcate apically; paired lateral plates slender, located in basal region of endosoma; without either ventral or basal plate. (Description of the genitalia is based on *flavonotatus.*)

Female: Sixth tergite pointed apically at middle in some species. Seventh segment well developed ventrally, covering eighth segment (valvifers) in most species. Eighth segment has first valvula well differentiated into outer and inner lobes; inner lobe well pigmented and short, folded beneath outer lobe; outer lobe simply narrowed apically, apex rounded and membranous; ramus extending basally along process of ninth tergite, which is provided with a crescent shaped sclerite apically. Second valvula pigmented on outer margin except for apex where is membranous, slightly constricted near apex, apex rounded and slightly extending beyond apical margin of intervalvular membrane where is rounded. Vulva short, simply rounded on apical margin. (Description of the female genitalia is based on *flavonotatus*?.)

Winged forms: Hemelytra with basal third subcoriaceous, venation as in *Rheumatometra* except for obliteration of lower vein in apical membranous region. Pronotum a little wider than long, widest at a little behind middle, posterior margin broadly rounded.

Distribution: New Guinea, The Solomon Islands.

The genus *Metrobatopsis* is somewhat similar to *Rheumatometra*, but differs from it by the following characteristics:

(1) The eighth abdominal segment in the male is strongly prolonged in most species. The ninth segment in the same sex with suranal plate has lateral spinous process, the pygophore is vertically rotated and the parameres are lost; while in *Rheumatometra* the eighth segment is not as greatly prolonged in two species of *Metrobatopsis (solomonensis, flavonotatus)*, the suranal plate is unmodified, the pygophore is not rotated, and the parameres are retained.

(2) The first antennal segment in male is longer and more strongly incrassate than in *Rheumatometra.*

(3) The front femur of the male is thickened near base but simply narrowed apically; in *Rheumatometra* it is greatly thickened and strongly arched.

(4) The dorsal surface of the head is only feebly widened in the female; in *Rheumatometra* it is greatly widened posteriorly.

(5) The mesonotum without a well impressed median longitudinal sulcus; in *Rheumatometra* the median longitudinal sulcus is well impressed in the female.

(6) The inner lobe of the first valvula is short; in *Rheumatometra* it is long and branched into two.

(7) The hemelytra have the lower (posterior) apical vein obliterated in *Metrobatopsis.*

Modification of the abdomen

Male: In relatively large species, *affinis,* the eighth segment is not prolonged although its ventral apical margin is provided with a pair of processes (fig. 1142), in the other two species (*solomonensis* and *flavonotatus*) the eighth segment is greatly prolonged and the ventral surface has a broad depressed area. The pygophore in *flavonotatus* and *solomonensis* is rotated vertically, exposing only the apical region of the pygophore; the suranal plate is also provided with a process on the lateral margin near apex in these two forms; in the larger species, *affinis,* the pygophore is not rotated vertically and without the process on the median longitudinal axis, and the suranal plate does not appear to have the lateral process (not dissected).

Female: In the female of an undescribed species the ventral apical margin of the seventh segment is simply concave (fig. 1138), and the eighth segment is exposed both dorsally and ventrally. This species is the largest in size. In the smaller species the seventh segment is greatly prolonged ventrally (figs. 1143, 1144), in *flavonotatus* the sixth tergite is acutely pointed on the posterior margin at the middle, and the seventh and eighth tergites are folded beneath the sixth tergite (fig. 1122), so is true with a species from the Solomon Islands (fig. 1144). In another species, however, the seventh and eighth tergites are well exposed without the sixth tergite being modified (1143).

Modification of the other structures

The antennae: In the relatively large and structurally primitive species, *affinis,* the first antennal segment of the male is simple; it is somewhat greatly thickened in the apical half in *solomonensis, flavonotatus* which are smaller.

The genus *Metrobatopsis* exhibits much more structural diversity than in the other genera of Trepobatinae, as noted from the foregoing account. We have already found also indication that the growth patterns for the antennal and leg segments are presumably considerably different at the specific level in this genus.

On Hermatobatinae

(Figs. 64, 1145-1151)

The Hermatobatinae was excluded from the Gerridae in an earlier part of this section (Classification). This group of water-striders are fundamentally different from the other groups of the Gerridae by the following highly unique characteristics:

(1) In the male the mesothorax and metathorax are completely fused both dorsally and ventrally.

(2) In the female the paired lobes arising from the anterior margin of the mesonotum develop posterolaterally as far as the apex of the abdomen, and the abdominal spiracles are placed laterally on the lobes.

(3) The vestigial dorsal scent gland openings are recognized on the basal region of the fourth abdominal tergite (figs. 1146, 1148).

(4) The pregenital abdominal segments are ventrally completely fused in the female and extremely reduced in the male.

(5) The front tarsus is distinctly three segmented.

(6) The eyes are granulated and the pronotum is extremely short.

TABLE 16.—Measurements of leg and antennal segments.

Gerrinae

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
Gerris (Aquarius) elongatus ♂	380	82:50:31:31	65:15	125:117:20:17	437:425:95:12	350:280:42:18
G. (A.) ventralis ♂	185	39:20:17:20	63:16	60:54:8:10	143:135:40:12	138:115:17:11
G. (A.) paludum ♂	210	47:19:16:19	50:14	60:55:9:12	185:162:47:14	187:120:26:12
G. (A.) antigone ♂	210	48:20:15:20	31:11	62:54:10:12	195:160:47:13	195:125:26:12
G. (A.) remigator ♂	192	40:17:15:18	....	59:53:8:10	170:145	185:105
G. (A.) conformis ♂	240	52:21:20:23	30:7	80:75:11:13	215:205:55:13	212:155:31:13
G. (A.) remigis ♂	242	41.4:20.3:20:23	55:17	78.2:68.2:12:13.3	180:156.8:64:17	173.3:143.5:37:13.3
G. (A.) nebularis ♂	248	42:20:18:23	29:7	79:70:10.5:12	207:190:53:14	205:130:28:13
G. (A.) nyctalis ♂	203	32:15:15:20	50:16	63:53:9:10	143:124:43:15	125:96:20:13
G. (A.) chilensis ♂	175	42:19:17:19	41:13	62:52:9.5:9.5	137:130:42:13	133:100:20:11
G. (A.) amplus ♂	275	53:27:25:26	70:20	86:80:14:18	217:168:65:16	190:165:37:14
G. (A.) spinolae ♀	232	....	40:12	63:54:10:12.5	187:150	213:122:27:14

G. (A.) uhleri ♂	210	45:20:16:20	24:7	63:57:9:10	180:148:43:13	195:125:25:12
Gerris (Gerris) gibbifer ♂	188	24:13:13:18	45:15	45:41:6:7.5	103:84:43:16	99:57:22:11
G. (G.) marginatus ♂	159	20:11:10.8:18.6	38:13	36.8:32.6:3.5:6	87.3:69.3:39:12.2	85.5:49.4:18:9
G. (G.) inseparatus ♂	148	21:12:11.5:17	....	35:33:3.5:6	90:68:37:13	88:50:17:9.5
G. (G.) incurvatus ♂	162	22:12:12:16	36:12.5	38:33:4:6	100:77:40:12	100:54:17:8.5
G. (G.) gillettei ♂	153	20:12:11:17	33:11.4	36:32:3.5:6.5	71:57:26:16	73:47:16:10
G. (G.) pingreensis ♂	138	17:10:8.5:13	32:12.5	33:30:3:6	73:57:25:14	72:42:15:9
G. (G.) buenoi ♂	120	19:10:9	32:11	32:29:3:6	77:62:35:12	72:39:12:8
G. (G.) argenticollis ♂	126	20:10:10:17	35:12	33:31:4:6	80:63:29:12	75:36:12:9
G. (G.) comatus ♂	160	23:12:11:16	37:13	39:36:5:7	98:76:40:13	93:56:19:10
G. (G.) incognitus ♂	130	18:10:10:17	32:12	34:30:3:6	75:62:31:14	72:48:16:9
G. (G.) firmus ♂	105	20:10:10:14	27:10	32:28:4:6	62:50:25:9	63:31:10:6
G. (G.) alacris ♂	145	23:12:12:15	35:12	37:35:4:6	90:70:37:12	87:52:18:9
G. (G.) odontogaster ♂	130	18:10:10:16	31:12	33:30:4:6	87:63:40:12	75:40:14:8
G. (G.) lacustris ♂	145	21:12:12:17	34:10	34:32:4:5	82:68:38:12	80:48:16:8
G. (G.) costae ♂	175	22:12:12:17	49:15.5	37:32:4:7	87:67:32:14	85:50:19:11

TABLE 16.—Measurements of leg and antennal segments.—*Continued*

Gerrinae

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
G. (G.) argentatus ♂	100	18:9:9.5:15	30:11.5	30:26:35:5	65:60:30:10	64:31:11:6
G. (G.) thoracicus ♂	178	22:11:11:16	36:12	37:36:4.5:6	93:75:35:15	90:54:18:10
Gerris (Limnoporus) canaliculatus ♂	137	25:18:18:28	53:12.5	37:33:4:6	97:83:35:10	109:43:10.5:6
G. (L.) rufoscutellatus ♂	235	43:30:23	70:17	62:53:8:9	150:113:67:15	178:112:30:13
G. (L.) notabilis ♂	295	55:38:28:31	82:18	83:70:12:12	197:167:100:21	235:150:43:19
G. (L.) dissortis ♂	225	40:29:22:31	65:15	62:53:8:8	140:120:73:17	180:110:34:13
Gigantometra gigas ♂	550	113:67:85:57	62:14	177:168:28:23	760:707:160:17	773:1.200:48:12.7
Gerriselloides brachynotus ♂	128	21:10.5:10.5:17	37:12	35:32:4:6	78:54:27:12	72:40:18:9
Gerrisella settembrinoi ♂	90	17:8.5:8.5:9.5	19:6	27:21.5:2:8	70:65:20:6.5	72:17:4.5:4
Eurygerris mexicanus ♂	128	22:18:19:19.5	30:7	41:39:8:8	82:79:45(?):9	80:49:21:8
E. flavolineatus ♂	92	16:13:13:13	28:7	38:28:5:6	75:71:40:7	74:38:12:7
E. carmelus ♂	118	21:17:17:16	25:6	39:35:6:6	83:75:40+:7	84:42:13:7.5

E. summatus ♀	118	20:18.5:20:18.5	23.5:6	38:36:7:7	87:75:47:8.5	94:45:20:7.5
E. cariniventris ♂	115	19:16:17:17	23:7	35:32:6:6	73:63:37:7	78:37:14:8
E. kahli ♂	135	21:17:21:19	30:7.5	39:36:7:7	87:80:45(?):8	90:48:22
E. fuscinervis ♂	110	17:11:12:16	23:7	37:32:6:6	80:75:37:8	80:43:14:7
Limnogonus guerini ♀	140 (158)	33:20.5:18:25	21.5:6	45:38:4.5:8.5	100:89:39:9	120:66:14:7.5
Limnogonus hesione ♀	106	26:13:14:13	14:6	34:30:2:6	83:77:34:8	76:42:12:5.5
L. celeris ♀	92	20:12:11:14	14:5	32:27:2.5:6	70:67:27:7.5	67:29:9:5
L. visendus ♀	96	19.5:11.5:11.5:11.5	13.5:6	32:27:3:6.5	82:74:24:8	77:30:8:4.5
L. lotus ♀	106	21:12.5:12:15	17:6	34:30:3:7	80:70:30:9	73:34:11:5
L. lubricus ♀	80	17:10:10:10	23:9	24:22:2:6	49:43:24:7	48:22:7:3.5
L. recens ♀	157	33:27:22:27	31:7	51:44:4:6	120:110:45:11	124:75:13.5:9
L. aduncus ♀	135 (135)	31:23:20:29	27:7.5	43:38:4:8.5	105:94:43:10	107:69:13:7.5
L. profugus ♀	133	28:18:17:24	25:7	40:33:4:5	90:84:42:9	90:69:15:8
L. ignotus ♀	127	24:15:14:20.5	20:6.5	34:30:3.5:6	82:73:30:7	82:43:8:5
L. hyalinus ♀	147	32:23:20:28	35:7	50:41:5:9	115:107:40:9	127:78:13:7.5
L. recurvus ♀	163 (145)	31:22.5:19:27	30:7	47:43:5:9	117:106:45:10	123:82:15:7.5

TABLE 16.—Measurements of leg and antennal segments.—*Continued*

Gerrinae

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
L. darthulus ♀	130 (128)	26.5:20:18.5:24	23:7	40:34:3.5:7	90:82:37:7	96:55:12:6
L. buxtoni ♀	135 (110)	27:18:17:23	27:7	42:37:5:8	107:98:45:10	112:73:13:8
L. australis ♀	150 (133)	26.5:18:18.5:22	24:7	50:43:5:8	123:110+:54:10	123:78:15:8
L. fossarum ♀	160 (145)	34:20.5:20.5:22	26:7	47:41:7:10	123:110:50:12	125:77:17:8
L. hypoleucus ♀	162 (152)	32:21.5:20:26	28:8	48:40:5:8	123:115:13:9	123:85:16:7
L. nitidus ♀	117 (132)	25:17.5:18.5:22	23:6	32:30:3.5:4	80:75:32:7	85:52:10:5
L. parvulus ♀	96 (95)	20:9:9.5:10.5	26:9.5	29:25:2.5:6	70:62:26:8	68:35:8:5
L. leptocerus ♀	133 (137)	31:21:18.5:22	23:7	42:35:4:6	97:93:40:8	103:63:12:5
L. cereiventris ♂	105 (105)	20:15:15:10.5	37:11	34:32:3:5	82:67:32:7	80:42:10:5
L. intermedius ♀	150 (148)	35:27	27:7	....	98:85:33:7.5	95:40:7:4
L. luctuosus ♀	145 (143)	30:21:19.5:26	27:7.5	43:37:5:8	112:100:45:11.5	115:65:13:7
L. lundbladi ♀	93 (93)	23.5:16.5:17.5:21	....	32:32:4:8	70:63:30:9	72:45:10:7.5

Tenagogonus (L.) ciliatus	292	88:62:53	55:11	112:98:18:12	327:346:90:18	354:220:43:14
T. (L.) cursitans ♂	282	64:48:43:45	45:9	92:82:17:9	265:262:72:14	283:175:36:12
T. (L.) femoratus ♂	310	63:47:63:72	50:10	108:96:18:15	330:315:83:12	318:318:43:12.5
T. (L.) nigripennis ♂	255	68:50:63:73	53:12	113:99:16:13	313:245:58:11.5	298:203:17:8
T. (L.) pulchrus ♂	275	60:47:60	47:11	102:89:16:11	263:290	297:228:33:10
T. (L.) annulicornis ♀	225	40:25:40:45	37:9	70:58:11:11	173:150(?):52:9.5	173:130(?):19:8
T. (L.) kallisto ♂	280	70:50:70(?):70	50:12	93:75:15:11.5	255:225:61:11	263:182:27:9
T. (L.) anadyomene ♂	163	45:33:42:47	37:9	67:58:8:9.5	180:140:50:10	172:110:22:9
T. (L.) palauanus ♀	138	90:55:60:90	25:6.5	49:40:7:6	115:100:35:9	115:63
T. (L.) borneensis ♂	230	48:32	35:8	70:62:13:11	210:167:55:12	137:97:30:9
T. (L.) rossi ♂	117	23:13:23:32	23.5:6	38:32.5:5:4.5	92:75:33:8	92:48:17:7
T. (L.) octopunctatus ♂	167	42.5:37:37(?):?	37:9	....	175:165(♀)	156:90+
T. (L.) fluviorum ♂	158	30:20:23:30	27.5:7.5	....	125:110:36:8	125:77:12.5:7
T. (L.) insularis ♀	168	46:37:49:56	35:7	56:46:10:9	146:129:45:7	147:83:17.5:7.5
T. (L.) minutus ♂	167	43:32:43	33:8	63:53:7:9	170:130:35(?)	168:90:17:9
T. (L.) lipovskyi ♂	200	63:58:48:47(?)	38:8	80:72:10:10	217:209:60:10	236:136:22:10

TABLE 16.—Measurements of leg and antennal segments.—*Continued*

Gerrinae

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
T. (*Tenagogonus*) *kuiterti* ♂	110	32:30:39:36	24:6.5	45:36:5:7	105:80:34:9	103:45:9:8
T. (*T.*) *kampaspe* ♂	78	23:19	19:6	30:27.5:2.7:4.5	70:62	73:35:9:5
T. (*T.*) *robustus* ♂	118	33:28:35:42	33:8.5	56:48:6:9.5	134:95:42:9	118:70:14:11
T. (*T.*) *divergens* ♂	132	34:30:45:50	32:7.5	53:43:6:10	....	....
T. (*T.*) *fijiensis*	92	31.5:22:21:24	19:6	45:40:5:8	98:85:26:8	103:60:8:6
T. (*T.*) *pravipes bergrothi* ♂	105	26.5:25:33:34	25:6.5	43:37:4:6.5	100:75:27:8	90:43:9:7
T. (*T.*) *madagascariensis* ♂	112	35:35:45:55	26:6.5	47:42:5:7.5	105:83:35:7.5	106:46:11:7.5
T. (*T.*) *albovittatus* ♂	113	32:34:42:45	28:8	48:40:6:8	117:97:32:8	111:50:11:6
T. (*T.*) *zambezinus* ♂	114	31:29:37:46	....	47:39:6:7.5	103.5:91:38 (1+2 segs.)	100:51:19 (1+2 segs.)
T. (*Tenagometra*) sp. ♂	105	31.5:24:18:22.5	50:14	43:37:6:8	108:101:43:8	102.5:55:12:7.5
Tenagometrella grandiusculus ♂	250	219:190:154:56	63:11	138:125:16:17.5	373:370:78:18	447:190:24:11
Do. ♀	213	75:62:55:50	47:9	78:68:12:12	206:205:52:13	220:120:19:9

Tenagogerris euphrosyne ♂	110	30:18:17:19	37:12	42:37:4:8	110:103:38:9	110:60:12:6
Tachygerris adamsoni ♂	113	22:16:26:39	26:6.7	37:34:6:6	92:72:42:8	90:40:12:6
T. spinulatus ♂	122	26:17.5:34:47	37:9	43:38:6:7	103:77:42:7	103:48:12.5:6.2
T. celocis ♂	106	22:17.5:34:44	28:6.2	37:30:5:5.5	90:68:44 (1+2 segs.)	86:32:14 (1+2 segs.)
T. opacus ♂	103	21:16:31:47	24:6	36:28:5:6	84:60:37:6.5	83:29:8:4
T. quadrilineatus ♂	118	24:19.5:26:44	30:8.5	40:35:6:6	95:68:45:7.5	98:45:15:6
T. surinamensis ♀	110	21.5:15.5:27:48	30:6.5	40:33:6:6	....	....
Charmatometra bakeri ♂	163	46:15:23:21.5	23:7	72:67:17:17	183:150:51:10	186:105:17:8.5
Eobates vittatus ♂	131	40:17:20.5:18	21:7	55:52:5:9	144:132:34:11	150:92:11:9
Brachymetra shawi ♂	135	27:15:19:17.5	22:5.5	48:44:6:9.5	117:125:36:8.5	140:80:18:8.5
B. kleopatra ♂	138	38:16.5:21:18	25:6.5	54:50:6.5:10	131:137:31:7	150:89:17:7.5
B. anduzei ♂	91	24:10:15.5:14	14.5:5.5	35:32:3:6.5	90:97:18:5	108:60:9.5:5
B. unca ♂	105	28:10:17:15	16:5	37:34:3.5:7	98:108:21:6	119:60:9:6.5
B. lata ♂	111	31:15:21:17	19.5:5.5	50:42:5:8	114:123:18:5.5	132:60:9:5.5
B. sp.	110	25:13.5:17.5:14.5	17:5.5	45:40:5:7.5	113:120:26:7.5	125:67:13:7

TABLE 16.—Measurements of leg and antennal segments.—*Continued*

Gerrinae

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
B. albinerva incisa	85	18:11:14.5:11.5	15:5	33:28:5.3.5:6	77:82:18.5:5.5	87:45:8.5:5
Cylindrostethus regulus ♂	360	42:16:11:19.5	14:5	69:60:5.5:10	195:147:55:12	195:130:7:5
C. palmaris ♂	280	35:15:10:18	13:5.5	62:56:4:12	176:134:50:15	170:110:7.5:5
C. linearis ♂	230	29:12:9:16	8.5:5	46:40:3:10	110:103:38:12	135:80:9.5:6.5
C. erythropus ♂	257	32:12:9:17	10:5.5	51:41:3:10.5	145:106:42:11	141:80:9:6
C. bilobatus ♂	220	30:12:9:15	9:5	47:41:3:10	133:102:37:11	142:92:8:6
C. hungerfordi ♂	320	....	15:6	68:60:5.5:13.5	190:150:66:12	193:136:7:4
C. bassleri ♂	275	35:13.5	10.5:5	53:47:3.5:10	169:126:48:12	160:96:11:7
C. productus ♂	405	64:25:16:22	18:8	93:83:45:13	310:203:125:21	310:237:13:6.5
C. sumatranus ♂	193	54:29:16:28	....	57:52:4:10	....	218:100:11:5.5
C. persephone ♂	186	31:17:11:15	....	50:50:3.5:11	183:121	195:95:10:7
C. vittipes ♂	145	23:15	9:5	39:40:2:8	160:97:31:10	170:70:6:6

C. costalis ♂	318	47:22:15:19	17.5:7	78:70:3:11	265:168:85:12.5	280:170:10:6
C. naiades ♂	188	29:16:10.2:17.5	....	50:50	196:113:40:11	215:86:12 (1+2 segs.)
Potamobates thomasi ♂	228	42:15:12:16.5	13:6.5	56:54:3.5:11	170:110:62:16	173:120:15:6.5
P. williamsi ♂	172	30:11:11:14	10:5.5	45:42:3.5:10	152:107:50:14	170:97:7.5:4.5
P. woytkowskyi ♂	193	31:11:11.5:17	12:5.5	47:45:3.5:10	162:112:52:13	168:100:10:4.5
P. horvathi ♂	143	25:11:9:14	10:4.5	37.5:36:2.5:8.5	140:92:38:11	140:74:7:4
P. peruvianus ♂	166	30:11:11:15	11:5.5	42:42:2.5:9	152:110:47:13	160:90:7.5:4.7
P. tridentatus ♂	160	28:12:12:14.5	10.5:5	44:40:2.5:9	147:103:38:12	152:82:6.5:4.5
P. unidentatus ♂	150	30:11:10:14	9:5.3	43:40:2.5:8.5	142:100:36:11	150:74:6:4.8
P. variabilis ♂	162	30:10:10:14	10.5:5.7	43:41:3:10	148:103:43:12	155:78:6.5:4.5
Platygerris asymmetricus ♂	110	32:11.5:7.5:15	7.5:5.7	40:36:4:11	178:64:41:12	200:51:14:7
P. caeruleus ♂	168	40:14:11:17	8.5:5.7	55:52:5:15	197:82:57:20	235:82:30:10.5
P. depressus ♂	100	28:9.5:7:11.5	6:5	35:32:3.8:9	157:58:37:11	165:47:11:6.5
Eotrechus kalidasa ♂	158	42:42.5	37:9	65:47:9:9	114:110	122:142
Onychotrechus sakuntala ♂	80	20:16:16:19	23:7	28:26:2.5:6	92:62:3:9	98:61:4:9

TABLE 16.—Measurements of leg and antennal segments.—*Continued*

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
Gerrinae						
O. rhexenor	83	22:16.5:15.5:17	14:5.5	27.5:25:2.7:5.5	86:58:3:9	92:53.5:3.5:8
Amemboa fumi ♂	64	16.5:13:14:19.5	14:5.5	21	57:38.5:	55:22.5:9.5:7
A. horvathi ♂	64	15:13.5:13.5:19	15:6.2	23:20:3:5	62:41:16:8	57:22:9.5:7
A. lyra ♂	60	15:12.7:14:20	12:6	20:17.5:3:5	54:38:15:8	50:21.5:9.5:6.5
A. sp. (from Thailand) ♂	70	16.5:13.5:16.5:26	13:6	21.5:19.5:3:5	57:40:17:7.5	54:24:11:7
A. sp. (from Thailand) ♂	68	13.5:12:12.5:19.5	15:6	20:18.5:3.5:5	50:36:15:7.5	48:20:9:6
Chimarrhometra orientalis ♂	123	30:20:19:21	26:7	41	103:70:22:10	90:50.5:12:9.5
Halobatinae						
Asclepios coreanus miyamotoi	45	17:10.2:8.5:8.5	5.7:2.3	21:17.5:2:7	58:47:20:9	52:27:3.5:6
A. apicalis ♂	47	19:10.3:8:8	4.5:2.5	17:14:1:6	52:41:17:7.5	46:23:2.5:5
A. coreanus ♂	57	20:10.5:8.5:9	5.5:3	22:18:1.5:8.5	63:57:22:9.5	58:32:5:4.7
Halobates sobrinus ♂	67	20:7.5:6.5:11	5.5:3.5	28:23:3:4	82:51:30:8	70:33:10.5 (1+2 segs.)

Halobates sericeus ♂	54	12.5:4.5:4.5:10	4.5:3	21.5:17.5:3.5:8	58:27:26:4	43:23.5:8 (1+2 segs.)
Halobates hawaiiensis ♂	87	30:10:7:9	6:3.5	33:27:4.5:5.5	95:70:35:11	80:40:11.5 (1+2 segs.)
Halobates splendens ♂	80	25:9:5:11.5	6:3.5	....	97:56:45:7.5	60:55:19 (1+2 segs.)
Halobates micans ♂	72	21:8:6:10	7.5:4.5	25:21:7:9	80:46:33:9	58:46:11 (1+2 segs.)
Halobates proavus ♂	56	21:8.5:6:9	....	32:26:5:12	70:48:27:10	63:28:8.5 (1+2 segs.)
Halobates germanus ♂	67	19.5:8.5:7:11	6.7:3.5	27:20.5:5:8.5	69:45:27:8	58:30:8.5 (1+2 segs.)
Halobates mariannarum ♂	75	....	6.3:3.5	30:25:9:8	93:62:28:9	77:38:10.5 (1+2 segs.)
Halobates flaviventris ♂	85	27:9.5:7:9	....	34:28:4:5	100:73	87:43:11 (1+2 segs.)
Metrocoris stali ? ♂	123	54:27:21:12.5	13:4.5	62:50:3:24	155:99:45:8	145:98:8.5:8.5
M. histrio ♂	91	43.4:18.1:16.3:11.9	....	44.7:39.1:16.1 (1+2 segs.)	114.0:92.3:42 (1+2 segs.)	119:77.1:14.2 (1+2 segs.)
M. nigrofasciatus ♂	65	26.5:11:13:10	....	30:25:2.5:20	75:56:30:6.5	69:44:4:6
M. strangulator ♂	87	39:19:16.5:10.5	15:5	44:39:2:15	110:71:35:6	103:62:6:6.5
M. lituratus ?	77	20:13	11:3.5	35:30:2.5:10	91:66:31:4	89:53:4.5:4.5

TABLE 16.—Measurements of leg and antennal segments.—*Continued*

Halobatinae

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
M. sp. (India) ♂	79	30.2:14:15:9	....	36:29:2:10	100:67:30:5	100:50:4:5.5
Eurymetra natalensis ♂	83	26:12.5:16:10	11:3	34:42:2.5:12	103:72:26.5:4	110:54:5.5:5
E. angolensis ♀	....	38:20:28:17	....	42:46:3:15	118:77:23.5:5	121:83:9:7
Eurymetropsiella schoutedeni ♀	65	23:14:11:9	....	30:23:7:12	97:62:30:?	87:36:4:5
Eurymetropsis carayoni ♀	61	21:13.5:11:9.5	....	32:22.5:18 (1+2 segs.)	96:55:25:5 (1+2 segs.)	82:35:4.5:5.5
Ventidius malayensis ♂	66	32:20:11.5:13.5	10:3	27:26:1.5(?):10	77:46:26.5:3.7	82:45:9:4.5
V. usingeri ♂	62	26:20:13:10	9:3.2	21:22:1(?):6.5	64:40:21:3	67:30:5.5:4
V. kuiterti ♂	42	20:6.5:7:8.5	5.7:2.5	18.5:15:0.8:1.5	50:27:14:3	55:19.5:3.7:1.5
V. werneri ♂	36	16:8:6.5:7	5:2	17:14:0.8:4.5	43.5:23:15:2.5	42:18:3.5:4
V. henryi ♂	41	17:7.5:5.8:5.8	5:2	18:15:1:4	47:29:16:3	54:20.5:3.2:4.8
V. chinai ♂	43	21:10:8:7.5	3.5:1.3 (♀)	21:16:1:5(♀)	53:31:17:4(♀)	57:25:4.1:4.1(♀)

Esakia usingeri ♂	45	22:6:7.3:6.5	....	20:17:0.5(?):5	60:37:15:3.5	67:20:3.5:4.0
E. kuiterti ♂	34	17:5.7:7:5.2	....	18.5:14.5:0.7(?):4	50:36:15:3.5	52:18:3.5:4.5
E. ventidioides ♂	....	21:6.5:8:6.3	....	....	59:42:13.5:3.2	67:17:2.8:4.8
Ptilomerinae						
Ptilomera (*Proptilomera*) *himalayensis*	180	110:27	21:6	108:91:42:22.5	270:175	320:200+
Ptilomera (*Ptilomera*) *pamphaga* ♂	275	120:31	....	132:115:72:29	380:252	450:330(?)
P. (*Pt.*) *lacustris* ♂	260	130:30:40:28	22:7	140:121:72:30	385:225:120:13	530:300(?):7 (1+2 segs.)
P. (*Pt.*) *phylactor* ♂	285	125:31:37:23	22:7	140:120:72:30	392:250(?)	478:270:7 (1+2 segs.)
P. (*Pt.*) *dromas* ♂	240	103:23:33:23	20:6.5	131:109:64:27	325:200(?)	365:220(?):6 (1+2 segs.)
P. (*Pt.*) *werneri* ♂	205	105:27:33:22	20:6	120:106:60:24	360:210:90(?):11	465:?
P. (*Pt.*) *aello* ♂	257	117:28:36:24	21:7	132:111:68:33	375:250	....
P. (*Pt.*) sp. (India)	233	112:29:34:24	....	122:108:68:26	330:225:90	391:300(?):5
Potamometra berezowskii ♂	230	100:23:29:21	22:10	130:112:87:26.5	428:255:150:13	490:355:9
P. tibetensis ♀	172	77:27	20:8	120:103:80:23	355	390

TABLE 16.—Measurements of leg and antennal segments.—*Continued*

Ptilomerinae

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
Rhyacobates chinensis ♂	105	58:15:17:11.5	9:6	58:52:17:10	170:95	180:50
R. takahashii ♂	100	56:15	9.5:5	57:48:16:10	162:80(?)	171:50(?)
R. lundbladi ♂	145	67:16:20:13.5	10.5:5	65:54:20:12	194:100:35(?):7	198:70(?):2:4
Heterobates dohrandti ♂	128	78:21:17:11.5	9:3.8	75:60:20:10	199:87:30(?):6	200:45:2:3
H. bilobatus ♂	130	60:16:13.5:10	7.5:4	57:46:18:10	161	168
Potamometropsis werneri ♂	125	54:21:23:13	12.5:4.5	63:50:17.5:11	175:80(?):30(?):9	183:50(?):1.6:3
P. hoogstraali ♂	134	60:17.5:24:17	16:5	76:64:20:12	183:100:40:10	183:90:1.7:5
P. obnubila ♂	107	62:20	10.5:4.5	....	....	....
Potamometroides madagascariensis ♂	108	58:19:19:12	....	65:54:18:11	180:100:30:6	166:43:2.5:3.5
Rheumatogonus burmanus ♂	83	22.5:19:14:11	7.5:2.5	38:26.5:5:6.5	100:60:20:5	102:30:1.5:2.5
R. intermedius ♂	73	21:14:13:11	7:3	33.5:25:5.5	87:55:20:5	88:25:1.5:2.5

Rhagadotarsinae

**Rhagadotarsus kraepelini* ♀	163	18:9:14:16	12.9	45:19:11 (1+2 segs.)	150:116.5:52:22	112:52:11:10
**R. hutchinsoni* ♀	194	27:7:12:15	12:9	47:19:10 (1+2 segs.)	118:95:33:20.5	108:43:9:10
**Rheumatobates petilus* ♀	100	13.5:5.5:10:12	10:4	27:13:10.5 (1+2 segs.)	70:59:30:10.5	47:27:3.5:8.5
**R. drakei* ♀	93	9.5:4:10:10	8:4	23:16:10 (1+2 segs.)	67:61:32:10.5	32:32:6:8
**R. bonariensis* ♀	81	7:3.5:7:9	9.5:5	19:12:9 (1+2 segs.)	62:59:31:10	40:23:4:6
**R. crinitus* ♀	99	10.5:5:10:12	....	25:13:10.5 (1+2 segs.)	67:55:29.5:10.5	46:26:5:9
**R. minutus* ♀	73	7:3.5:9.5:8	8:4	18:11:7 (1+2 segs.)	44:36:16:7	31:20:8 (1+2 segs.)
**R. mangrovensis* ♀	115	15.5:6:9:12	13:6	29:15:11 (1+2 segs.)	79.5:55:32:12	55:31:4:7
**R. trinitatis* ♀	131	15.5:7:10:21	14:8	33:17:14 (1+2 segs.)	89:73:41:14	58:34:5:15
**R. creaseri* ♀	108	9.5:4:10:12	....	23:12:10	69:62:36:11	48:31:7:10
**R. citatus* ♀	93	8:3.5:10:10	11:4.5	23:12:10 (1+2 segs.)	61:56:31:11	48:27:7:10

TABLE 16.—Measurements of leg and antennal segments.—*Continued*

Rhagadotarsinae

Name of species	Length of body	Antennae 1:2:3:4	Rostrum	Front leg	Middle leg	Hind leg
**R. praeposterus* ♀	94	....	....	22:11:10 (1+2 segs.)	60:60:33:10	47:29:7:8.5
**R. tenuipes* ♀	112	10:5:12:12	12:6	29:16:11 (1+2 segs.)	82:74:33:14	51:36:9:11
**R. hungerfordi* ♀	106	9.8:3.5:11:13	13:6	25:13:10.5 (1+2 segs.)	65:60:33:12	48:30:8:10
**R. trulliger* ♀	110	10:5:12.5:11	12.5:6	24:13.5:10 (1+2 segs.)	76:67:31.5:15	48:32:9:10
**R. rileyi* ♀	100	9:3.5:10.5:10	....	22.5:11:10 (1+2 segs.)	70:61:31:15	40:31:11:10
**R. klagei*	110	13:4:10:13	11:5.5	30:12:10 (1+2 segs.)	79:81:34:18	50:33:5:16
**R. imitator*	103	10:4:12:10	12:6.5	23:11:10 (1+2 segs.)	67:62:31:12	42:32:8:10
**R. mexicanus*	92	9:3:12:10	12:7	22:11.5:10	62:52:29.5:11	40:26.5:6:10
**R. crassifemur esakii*	101	10.5:4:10.5:15.5	11:5.5	27:12:10	78:82:32:18	51:34:5:10

Trepobatinae

Metrobates fugientis ♂	61	22:6.5:5.5:7	7:3.5	23:15:1:7	41:78:12:10	72:20.5:1.8:8
M. trux infuscatus ♂	72	27.5:9:5:7	7:3.5	26:18:1.7:8	62:92:13:21	87:29.5:2:9.5
M. hesperius depilatus ♂	67.5	28.5:12:7:8	....	28:20:2.5:8.5	61:93:15.5:22	96:32:2:8
M. plaumanni ♂	72	32:14:9:6	7:3.5	32:23:3:10	57:106:17:22	87:30:3:9
M. porcus ♂	60	20:6.5:4.5:6.5	6:2.7	24:13.5:1.5:7	52:92:12:18	88:23.5:2:7.5
M. denticornis ♂	65	22:7:5:6	6.5:3.5	24.5:16:2:8	57:94:11:22	78:29.5:2:9
M. artus ♂	67	24:9.5:6:7.5	7:3.2	24:17:1.5:8.5	53:89.5	79:34:2:10
M. anomalus ♂	65	24:10.5:7:8.5	7:3.5	27:19:2:7.5	57:91:13:22	87:31:2:8.5
M. tumidus ♂	58	21:6.5:5:6.5	5.5:3	22:15:1.5:6	46:89:11:20	80:24:1.5:8
**Trepobates floridensis* ♂	115	32:18.5:19.5:20.5	18:8	55:34:2.5:14	60:119.5:37:30.5	92:43:17:11
**T. inermis quadratus* ♂	120	32:15:18:20	18.5:8.5	52:35:4:14	65:129:45:31	98:47:20:11
**T. subnitidus rotundatus* ♂	121	35:17:20:22	19:9.5	52:38:2.5:15	66:130:40:33	100:46.5:19:12.5
**T.* sp. ♂	117	32:17.5:20:22	15.5:9.5	50:35:2.5:17	64:123:38:31	91:43:17:12.5
**T. pictus* ♂	115	39:20:21:22	....	50:37	67:120:37:30	88:47:28
**T. trepidus* ♂	137	33.5:18.5:19.5:20.5	20:10.5	53:40:3:16.5	71:137:41:35	107:50.5:20.5:13.5

TABLE 16.—Measurements of leg and antennal segments.—*Continued*

Trepobatinae

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
**T. vazquezae* ♂	133	42:21:22.5:23	20:10	60:38:3.5:18	72:132	101:50:22:13.5
**T. knighti* ♂	130.5	34:18.5:20:21	19:8.5	52:35:3:14	68:128.5:73 (1+2 segs.)	101:45.5:31 (1+2 segs.)
**T. taylori* ♂	113.5	33:15:18:20	18:11	....	62:119	89:45
**T. inermis* ♂	112	35:19:21:21	13.5:8	....	63:117.5:35:30	90:47:17:12
Trepobatoides boliviensis ♂	64	26:10:11:14.5	9.5:4	27:18:1.3:6	48:75:23:12	60:30:5:6
Telmatometra whitei ♂	75	19:11:23:18	14:5	31:26:1.8:6	57:83:25:19	70:38.5:7:8
T. ujhelyi ♂	69	17:10:32:18	15.5:5.5	31:25.5:2:8	63:79:23:17	62:32:6.5:7
T. indentata ♂	57	13:8:20.5:16.8	11:4.7	22.5:19:1.5:7	40:59:17:14	50:21:4:5
T. parva ♂	53	13:7:21:19	11:4	22.5:19:1.3:6	36:54:17:12	46:18.5:4:5
T. fusca ♂	61	13:8.5:20:19	11:4.5	24:19:7:5.5	36:51:18:16	45:20:4:5
T. retusa ♂	52	13:8:20:18	13.5:5	24:20:1.5:7.5	47:67	52:30(?)
T. acuta ♂	61	14:9.5:22:20	12:4.5	25:21:1.2:6	40:60:20:13	52:23:5.5:5.5

Halobatopsis platensis ♂	60	13.5:7.5:11:13.5	8.8:4	22:17:1.5:7	42:63:21:17	50:22.5:4.5:5.5
H. spiniventris ♂	71	17:8.5:11.5:11	11:4.7	27.5:21:2.0:8.5	47:70:23:17	58.5:30:7:6
Ovatametra fusca ♀	40	7.5:5:6:8	6:3.3	14:10	20:33.5:12.5:12.5	25.5:15:6:4.5
O. obesa ♀	52	10:6:6.5:9.5	8:4	16:13.5:1.2:3.5	26:43:16:13	31:15.5:6:4
O. minima ♂	34	7.5:4.3:4.7:6.5	5.5:3	12:10:1(?):3	18:28:10:8	21:10.5:4:3.5
**Rheumatometra philarete* ♂	97.5	24:17.5:12:12	....	....	57:72:37:18	62:27:11 (1+2 segs.)
Hynesionella omercooperi ♂	40	8.5:6:4.8:5.1	5.5:3.2	11:8.5	22:33:10.5:10.5	25.5:10.5:1.5:4.5
H. aethiopica ♂	54	12:9.5:8:8.5	....	19:15:2.5:9	51:73:33:13	52:25:11 (1+2 segs.)
Naboandelus signatus ♀	42	8.5:5.5	5.5:3	11.5:8.8:0.8:4	25:37.5:12:9	28:11:2.5:4
N. bergevini ♀	44	....	....	15:11:1.2:5	32:45:16.5	38:15.5:2.5:5.5
N. sp. (Formosa) ♀	34	7.5:6.5:6.2	4:2.8	....	30:40:14:10	....
Stenobates biroi ♂	72	25:12:9.5:10	10:6	22:19:2.5:12	60:72:25:21	66:23:4:6
Rheumatometroides browni	55	13:9:7:9	....	17:14:2:7	41:51:16:15	42:17:3:5.5
Cryptobates raja ♀	54	13:8:17.5:16.5	15:5	20.5:18:2:7	42.5:50:16.5:12	45:21:5:5
C. kuiterti ♀	44	7:4	....	16:13.5:1:4	27:36:12:10.5	31.5:13.5:4:5

TABLE 16.—Measurements of leg and antennal segments.—*Concluded*

Trepobatinae

Name of species	Length of body	Antennae	Rostrum	Front leg	Middle leg	Hind leg
		1:2:3:4				
Metrobatopsis flavonotatus ♂	73	23:15.5:9:10.5	....	27.5:20:2:8	61:83:45:20	80:29:11 (1+2 segs.)
M. affinis ♂	97.5	24:17.5:12:12	....	....	57:72:37:18	62:27:11 (1+2 segs.)

The lengths of body in parentheses for the species of *Limnogonus* are the individuals from which the measurements of antennal segments were made.

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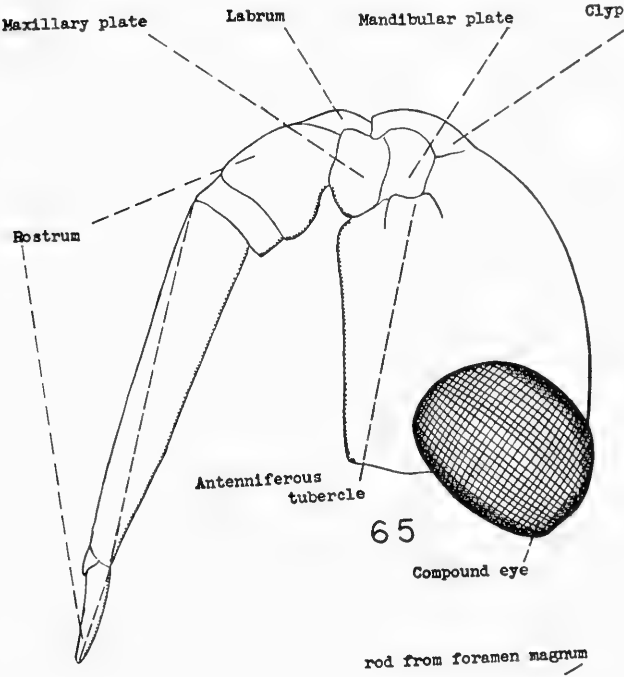
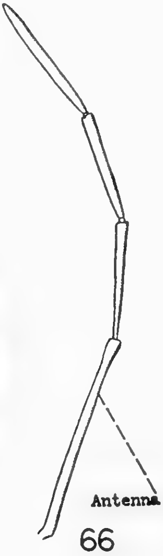
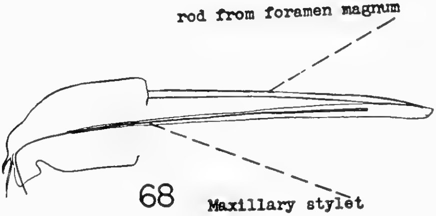
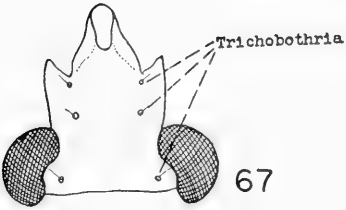
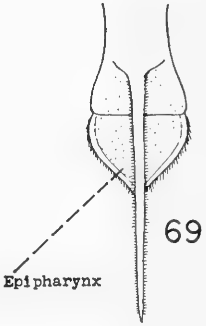
FIGURES 65-69





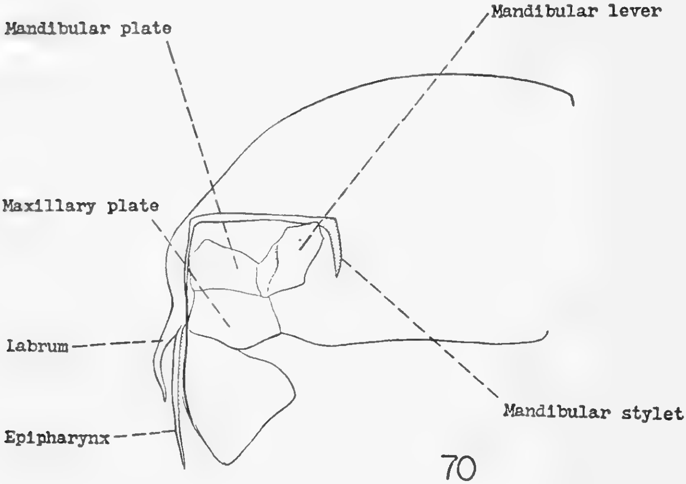




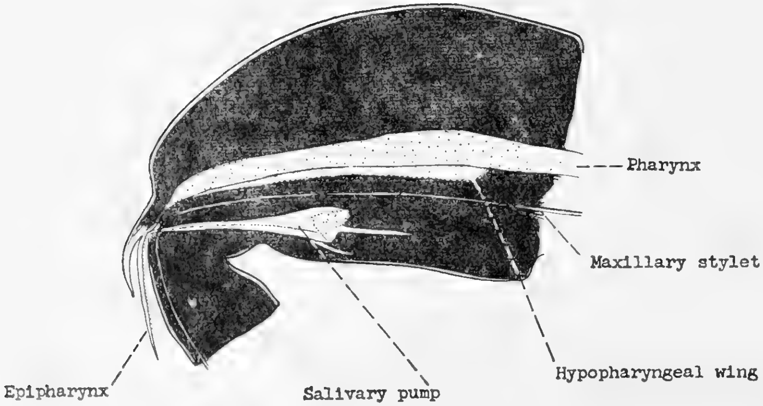


65. Lateral view of the head, *Gerris remigis* Say.
66. Lateral view of the antenna, *Gerris remigis* Say.
67. Dorsal view of the head, *Gerris remigis* Say.
68. Sagittal section of the head, *Gerris remigis* Say.
69. The epipharynx, *Gerris remigis* Say.

FIGURES 70, 71



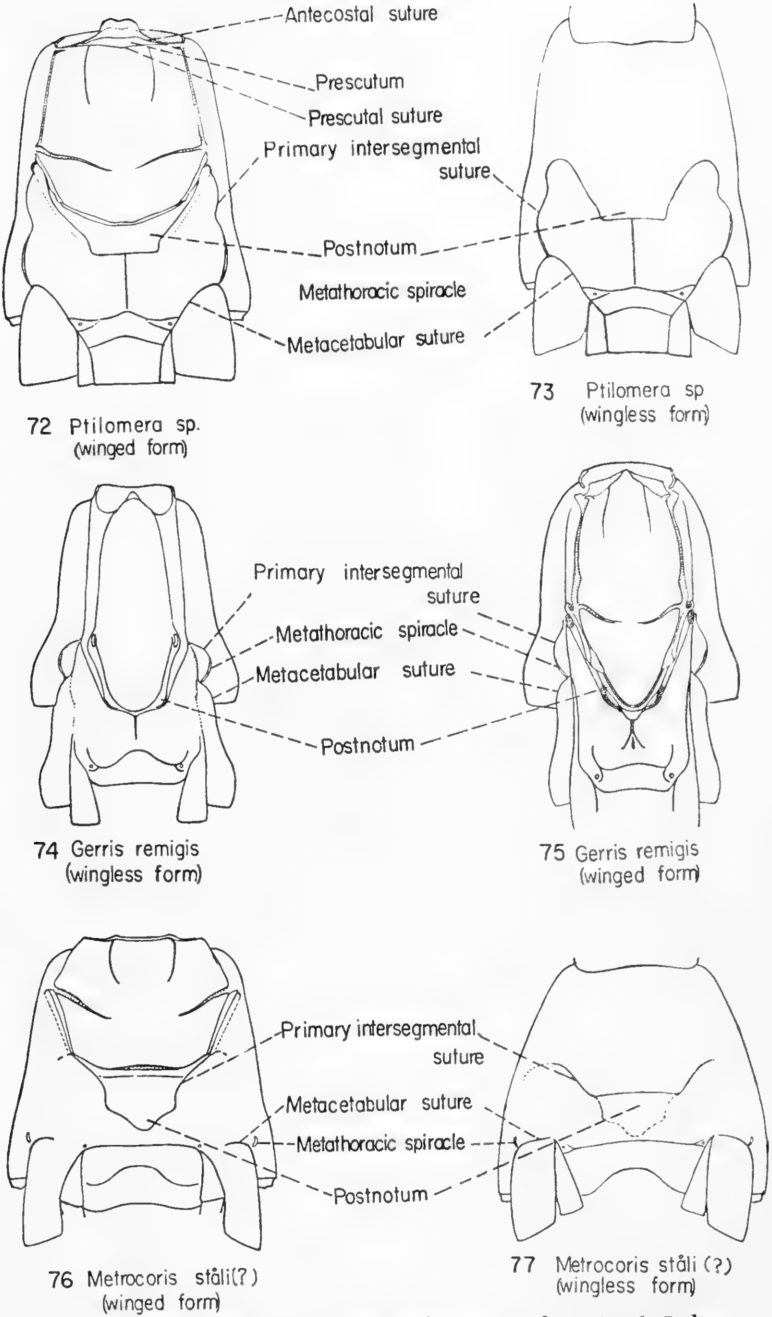
70



71

70, 71. Sagittal sections of the head, *Gerris remigis* Say.

FIGURES 72-77



72 Ptilomera sp. (winged form)

73 Ptilomera sp (wingless form)

74 Gerris remigis (wingless form)

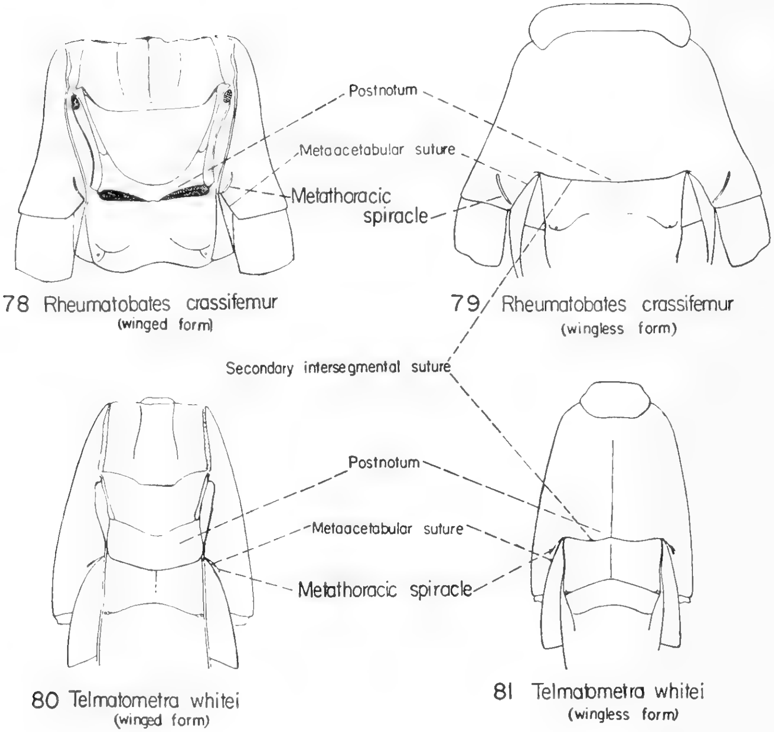
75 Gerris remigis (winged form)

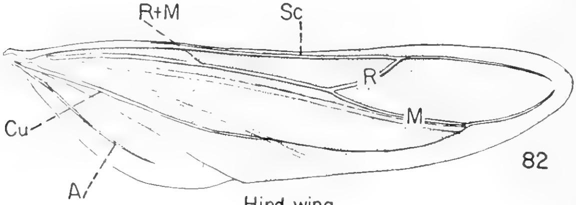
76 Metrocoris stâli(?) (winged form)

77 Metrocoris stâli (?) (wingless form)

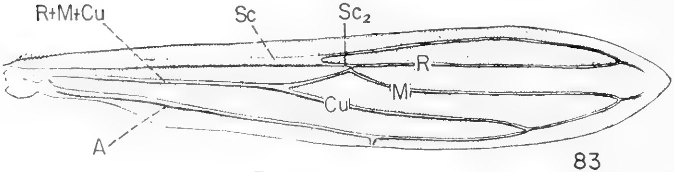
72, 73. Dorsal view of the thorax, *ptilomera* sp. from South India.
74, 75. Dorsal view of the thorax, *Gerris remigis* Say.
76, 77. Dorsal view of the thorax, *Metrocoris stâli* (Dohrn). (?)

FIGURES 78-83





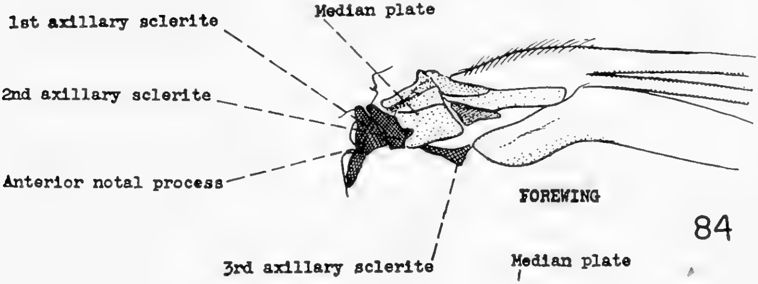
Hind wing



Forewing

78, 79. Dorsal view of the thorax, *Rheumatobates crassifemur* Esaki.
80, 81. Dorsal view of the thorax, *Telmatometra whitei* Bergroth.
82. The hind wing, *Gerris remigis,* Say.
83. The forewing, *Gerris remigis* Say.

Figures 84-87



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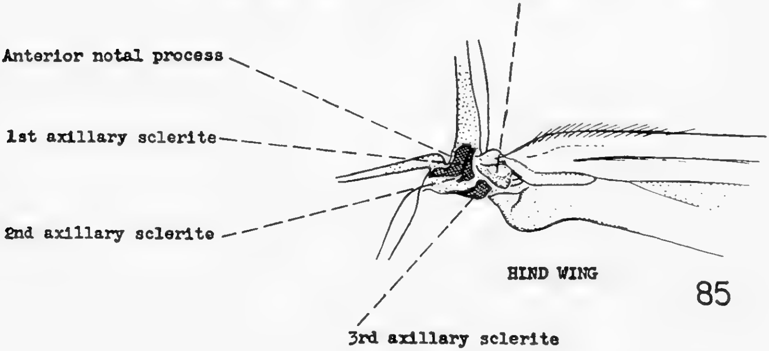

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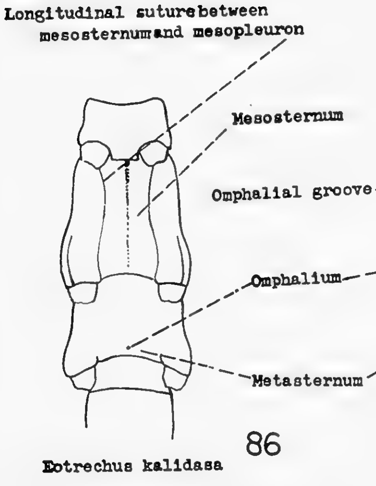

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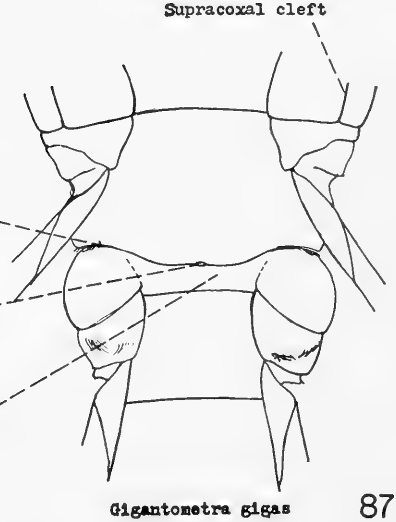
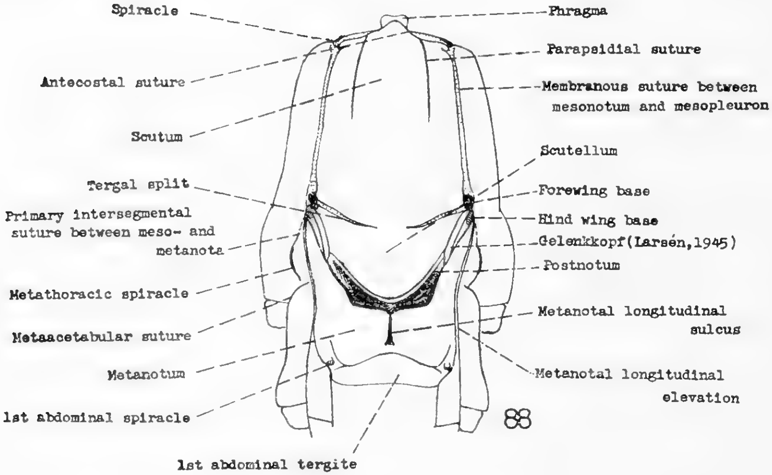


87

84. The forewing base, *Gerris remigis* Say.
85. The hind wing base, *Gerris remigis* Say.
86. Ventral view of the thorax, *Eotrechus kalidasa* Kirkaldy.
87. Ventral view of the thorax, *Gigantometra gigas* (China).

FIGURES 88-90



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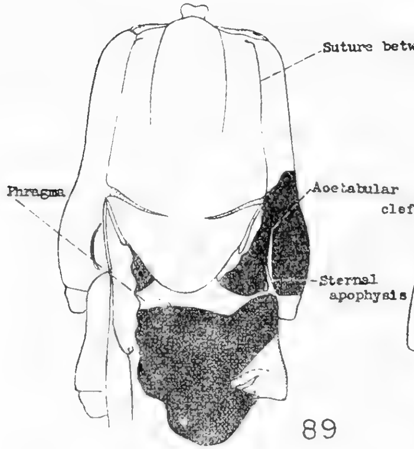

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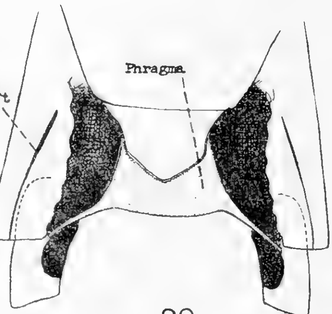


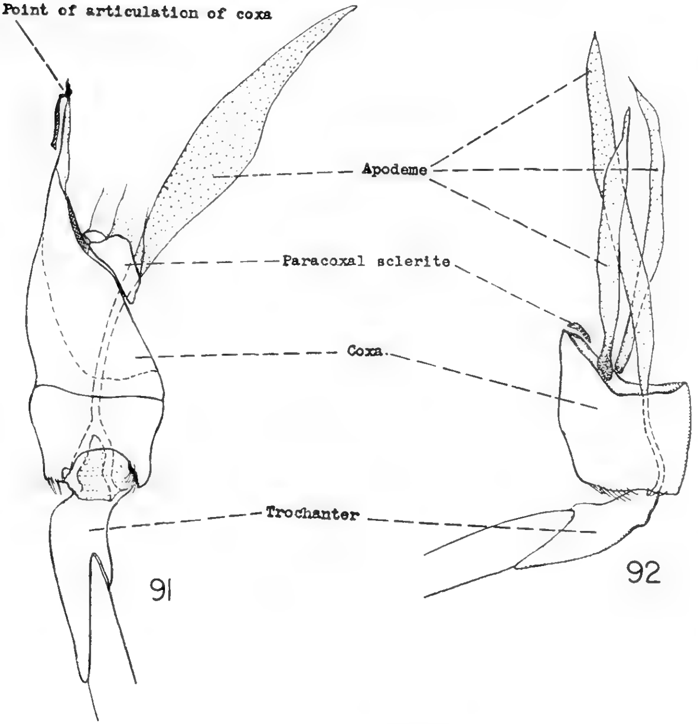
90

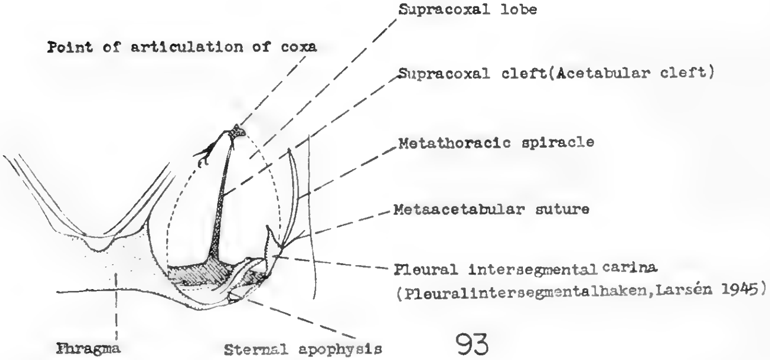
88. Dorsal view of the thorax, *Gerris remigis* Say.

89. Dorsal view of the thorax, showing internal structures, *Gerris remigis* Say.

90. Dorsal view of the thorax, showing internal structures, *Metrocoris ståli* (Dohrn) (?).

FIGURES 91-93





91. Middle coxa, *Gerris remigis* Say.

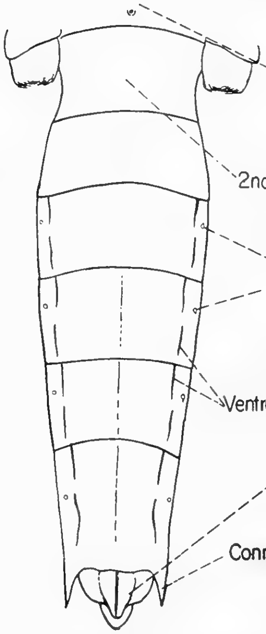
92. Hind coxa, *Gerris remigis* Say.

93. Dorsal view of the metathorax, showing internal structures, *Gerris remigis* Say.

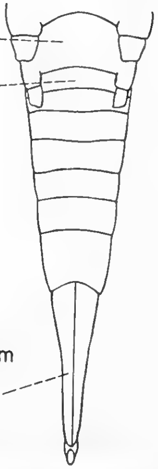
FIGURES 94-97

94. Ventral view of female abdomen, *Gerris remigis* Say.
95. Dorsal view of the body, *Gerris remigis* Say.
96. Ventral view of the female abdomen, *Rhagadotarsus kraepelini* Breddin.
97. Dorsal view of body, *Rhagadotarsus kraepelini* Breddin.

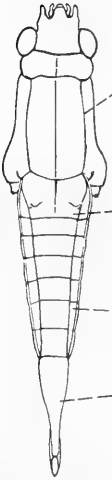
Figures 94-97



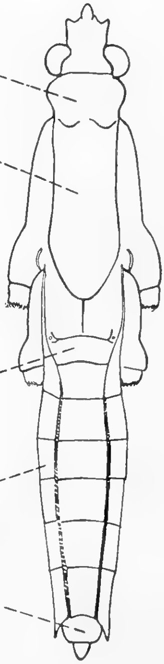
94 Gerris remigis



96 Rhagadotarsus kraepelini



97 Rhagadotarsus krapelini



95 Gerris remigis

FIGURES 98-101

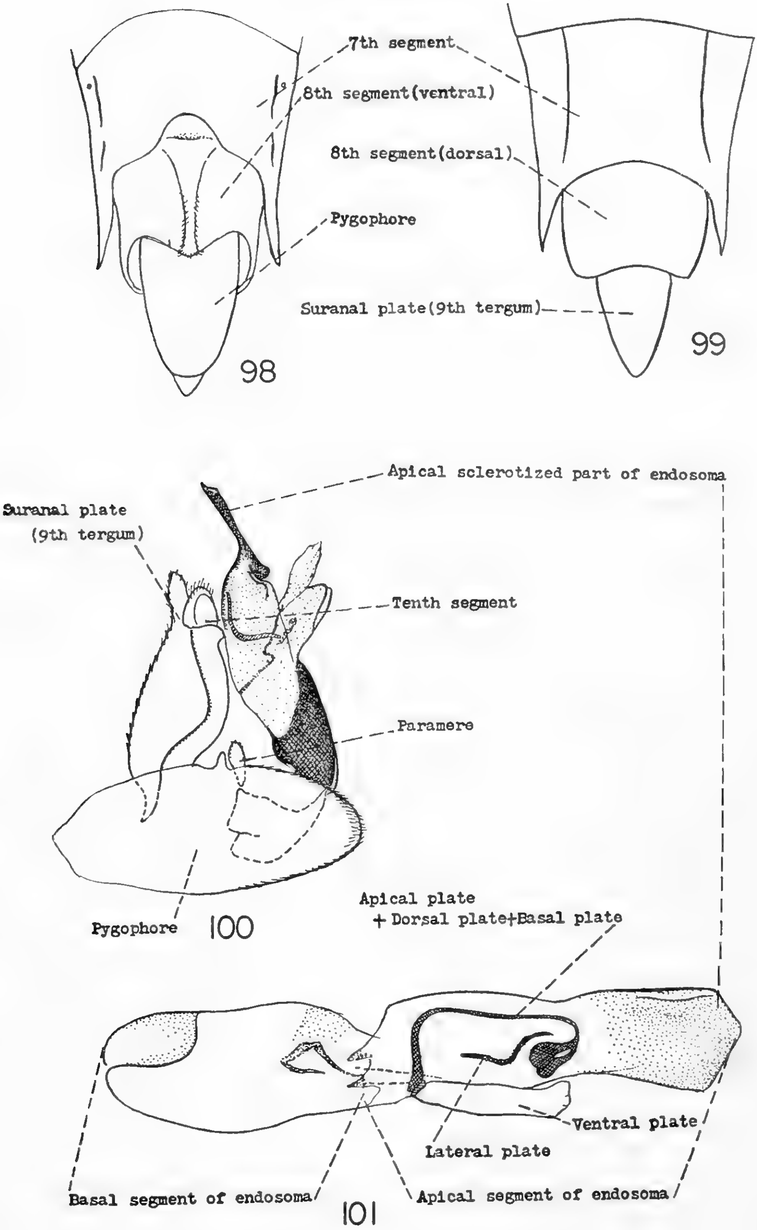
98. Ventral view of male apical abdominal segments, *Gerris remigis* Say.

99. Dorsal view of the male apical abdominal segments, *Gerris remigis* Say.

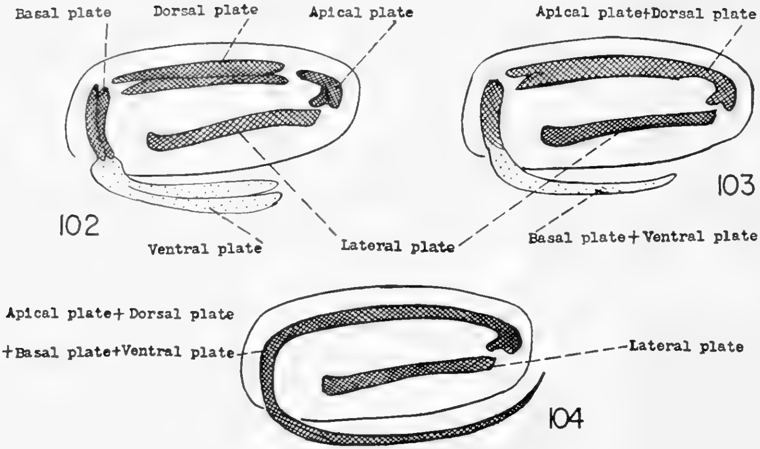
100. Lateral view of the male ninth and tenth abdominal segments, *Gerris remigis* Say.

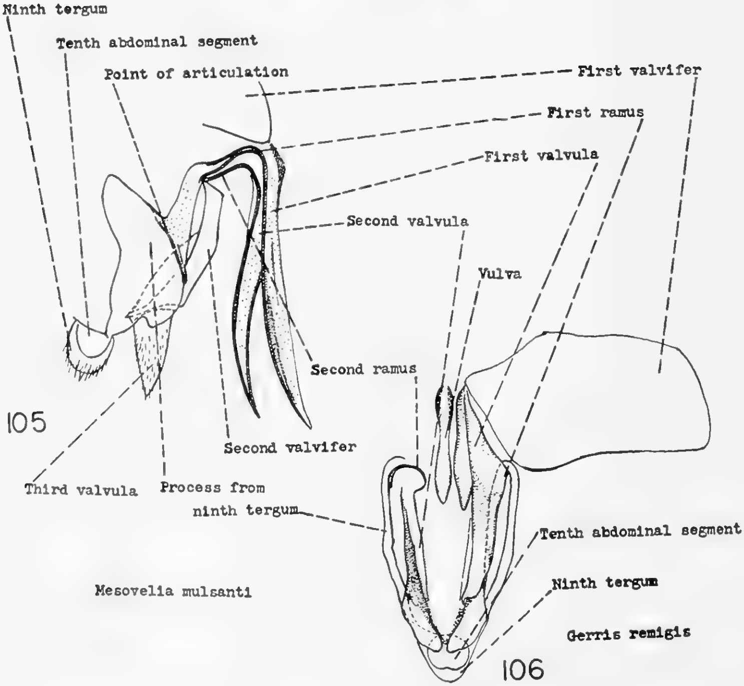
101. Endosoma, *Gerris remigis* Say.

FIGURES 98-101



FIGURES 102-106



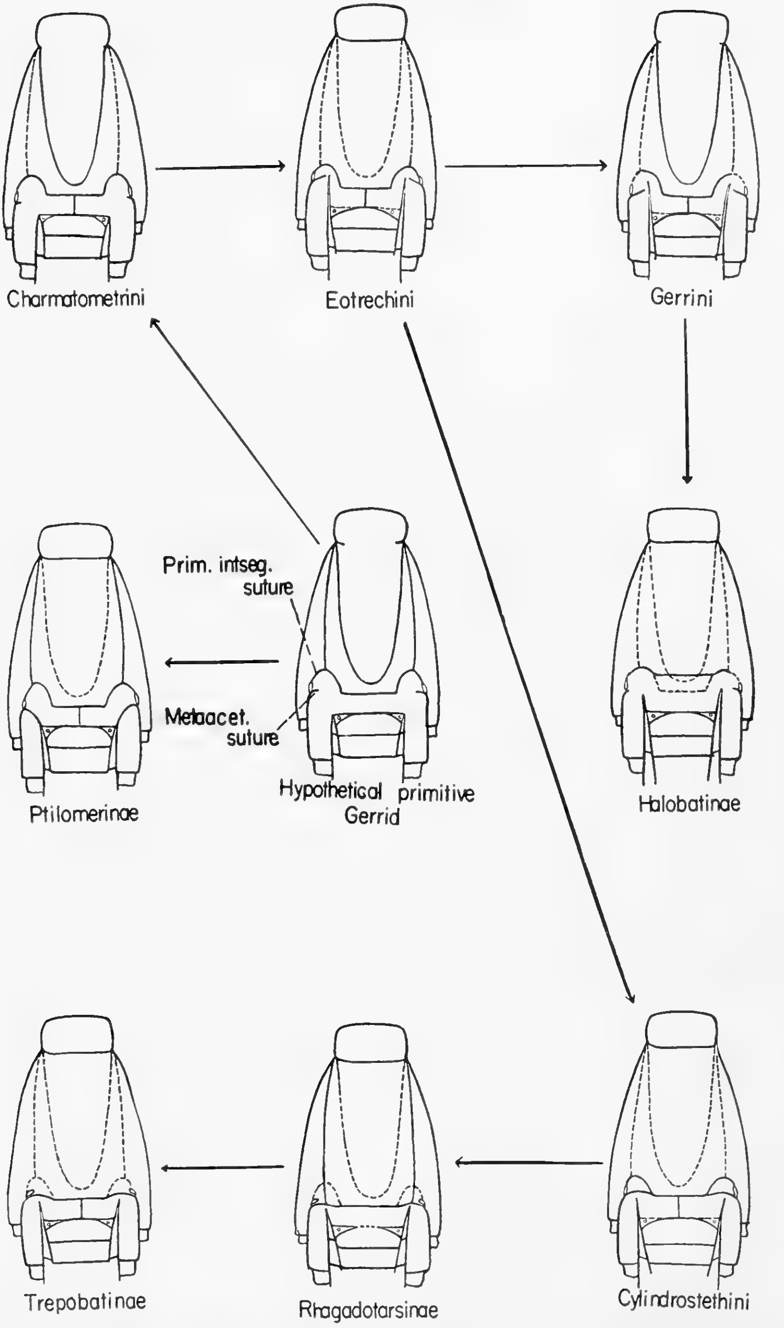


102.-104. Diagrammatic drawings of sclerotized plates in endosoma of Gerridae.

105. Female genitalia, *Mesovelia mulsanti* B.-White.

106. Female genitalia, *Gerris remigis* Say.

FIGURE 107



107. Diagram showing evolution of thoracic and basal abdominal sutures in Gerridae. Broken lines indicate the sutures that have been lost.

Figure 108

108. Postembryonic growth of antennal segments in *Metrocoris histrio* B.-White, broken lines are for female. Each connected point is mean value at different stages.

FIGURE 108

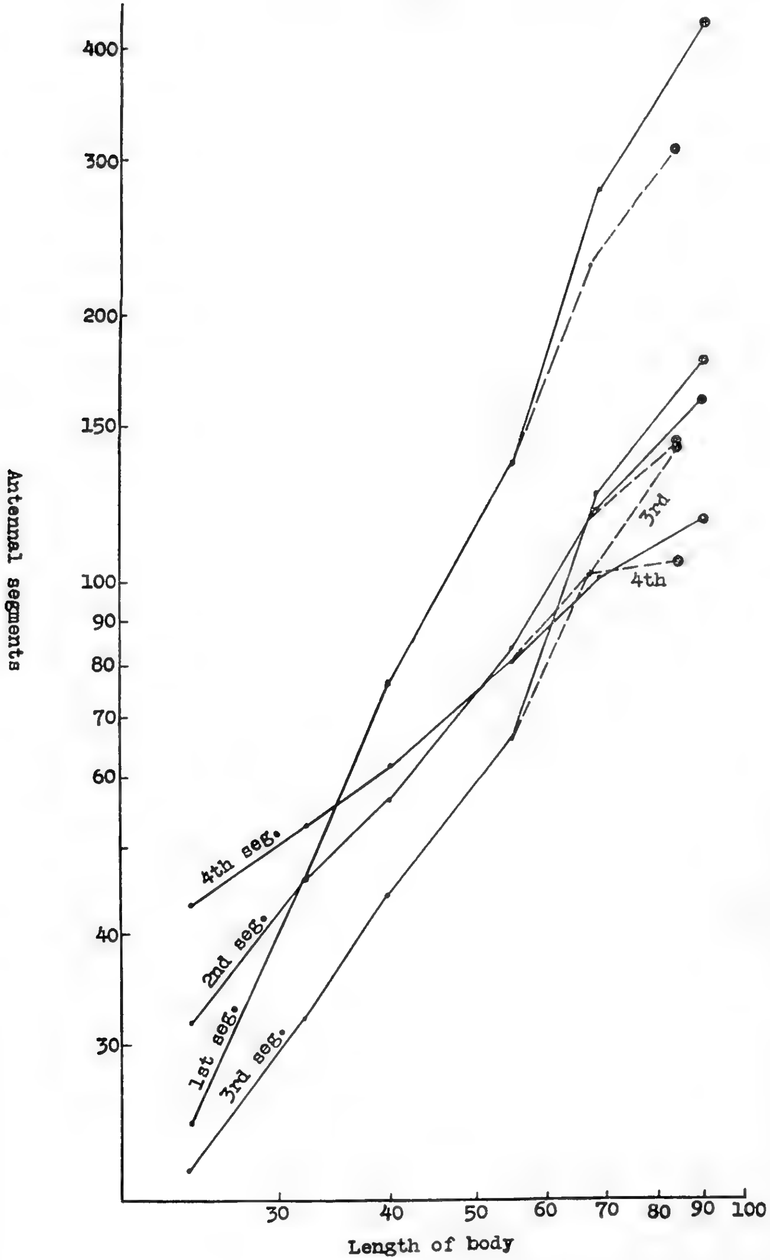
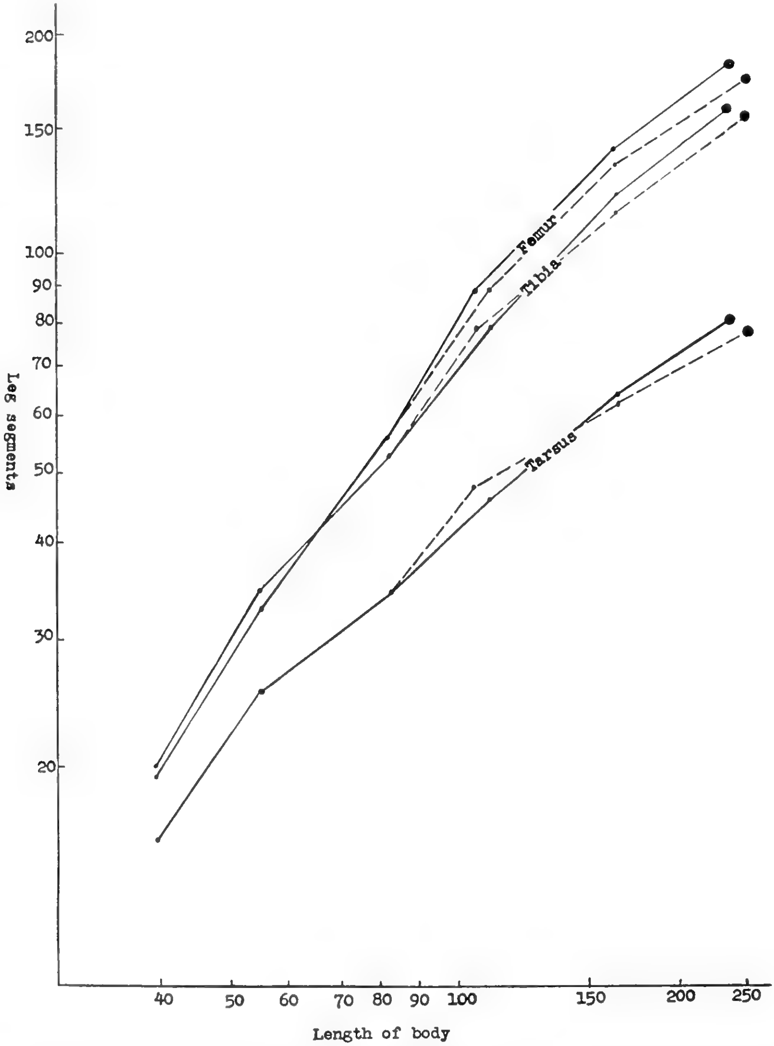
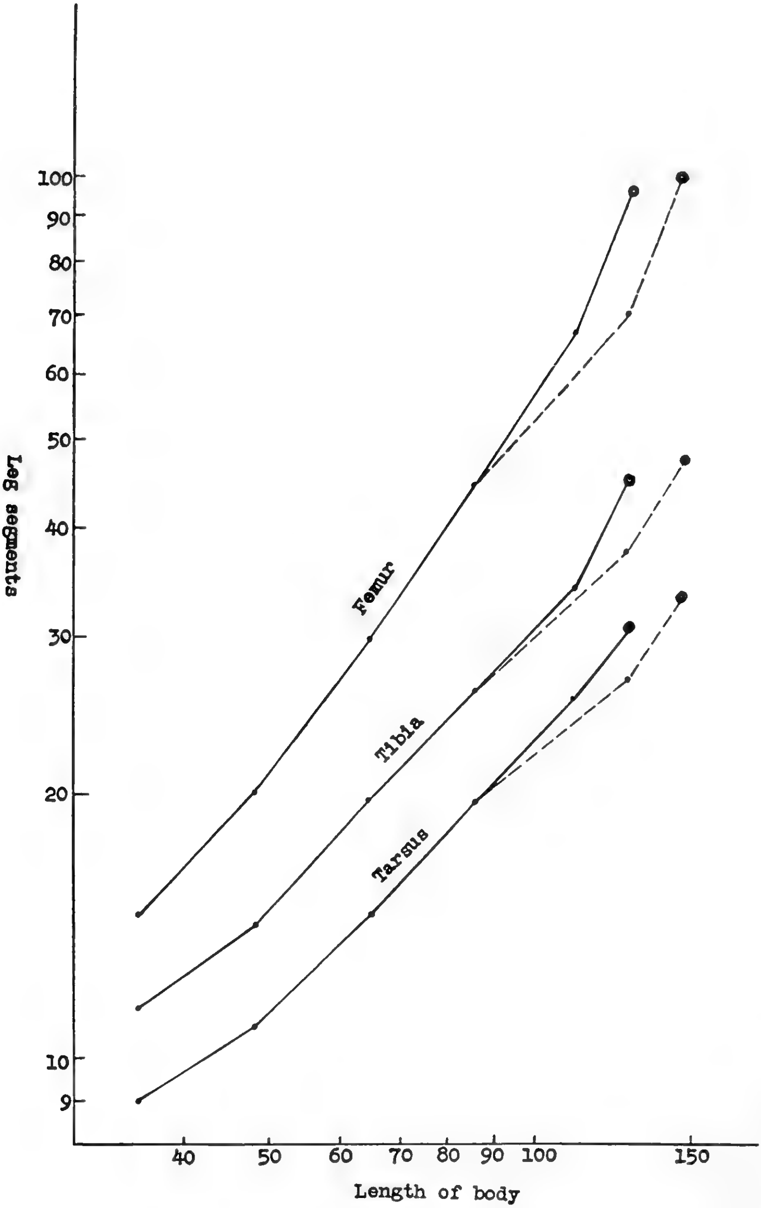

400
300
200
150
100
90
80
70
60
40
30
Antennal segments
4th seg.
2nd seg.
1st seg.
3rd seg.
3rd
4th
30
40
50
60
70
80
90
100
Length of body

FIGURE 109



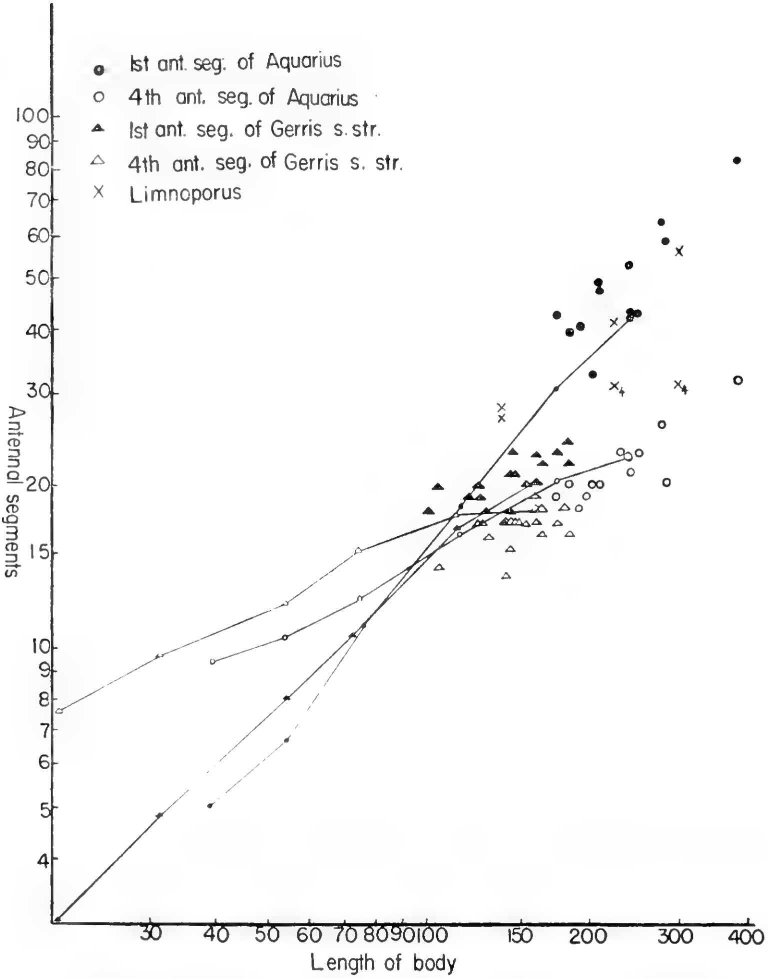
109. Postembryonic growth of hind leg segments in *Gerris remigis* Say. Broken lines are for female. Each connected point is mean value at different stages.

FIGURE 110



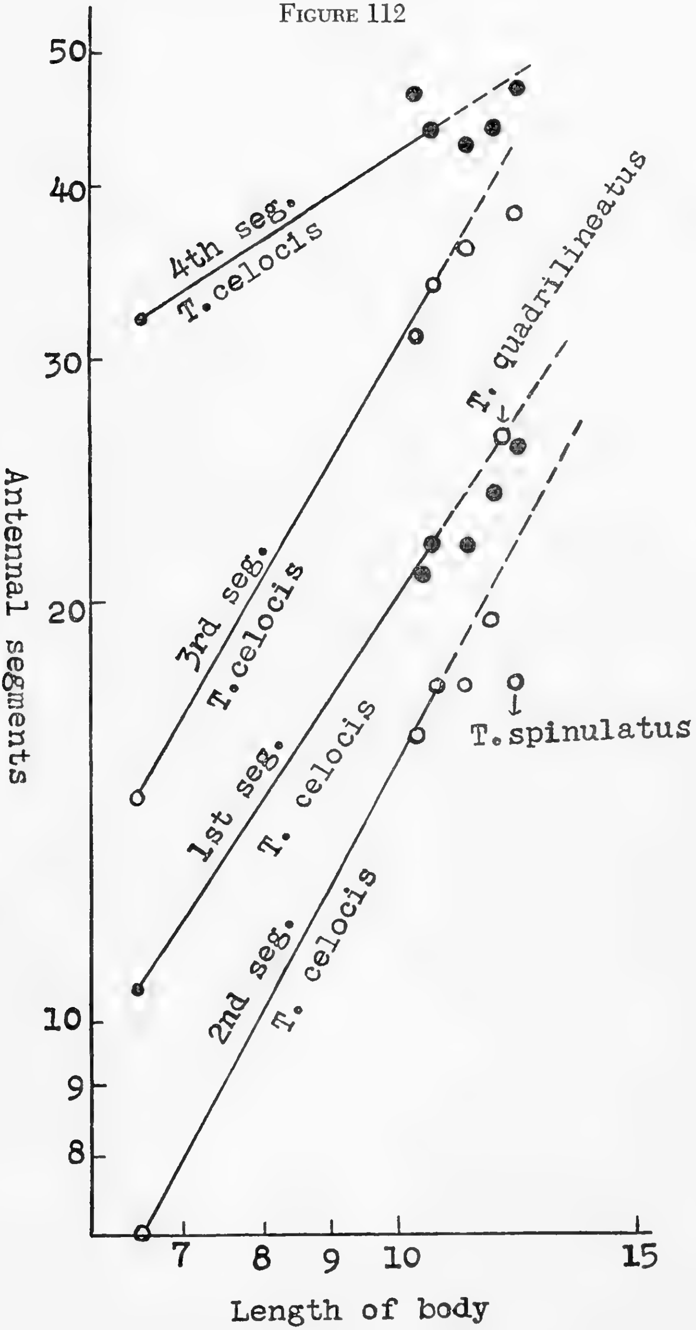
110. Postembryonic development of the hind leg segments in *Trepobates Knighti* Drake. Broken lines are for females. Each connected point is mean value at different stages.

FIGURE 111



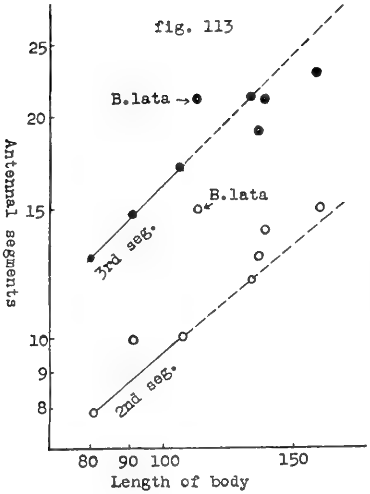
111. Antennal segments in *Gerris*. Each connected point is mean value at different stages.

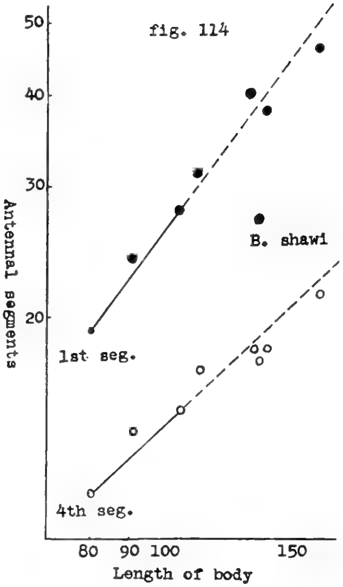
Figure 112



112. Antennal segments in *Tachygerris.*

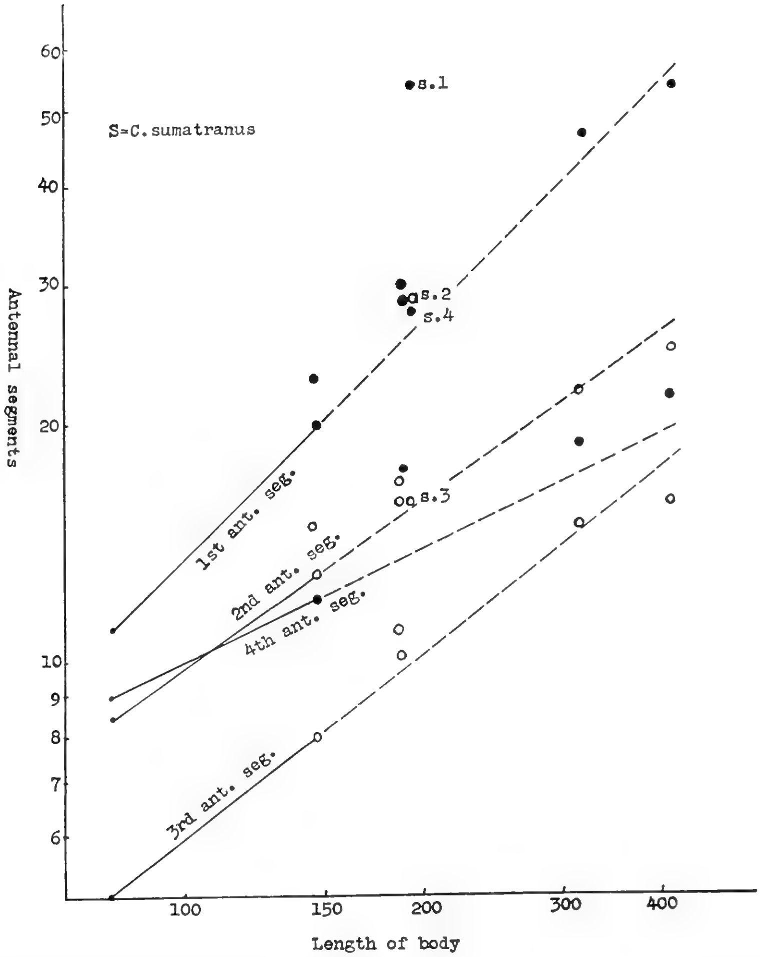
FIGURES 113, 114





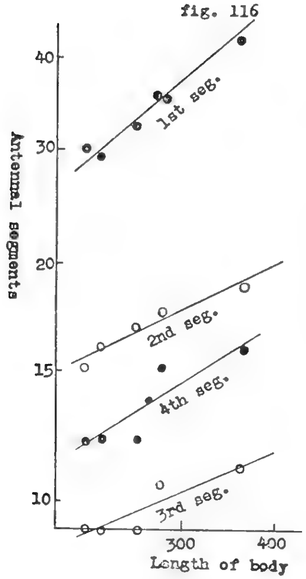
113. Second and third antennal segments in Charmatometrini.
114. First and fourth antennal segments in Charmatometrini.

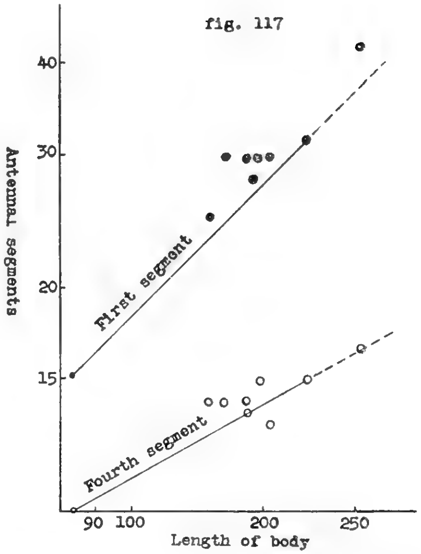
Figure 115



115. Antennal segments in *Cylindrostethus* from the Eastern Hemisphere. S. is *Cylindrostethus sumatranus* Lundblad.

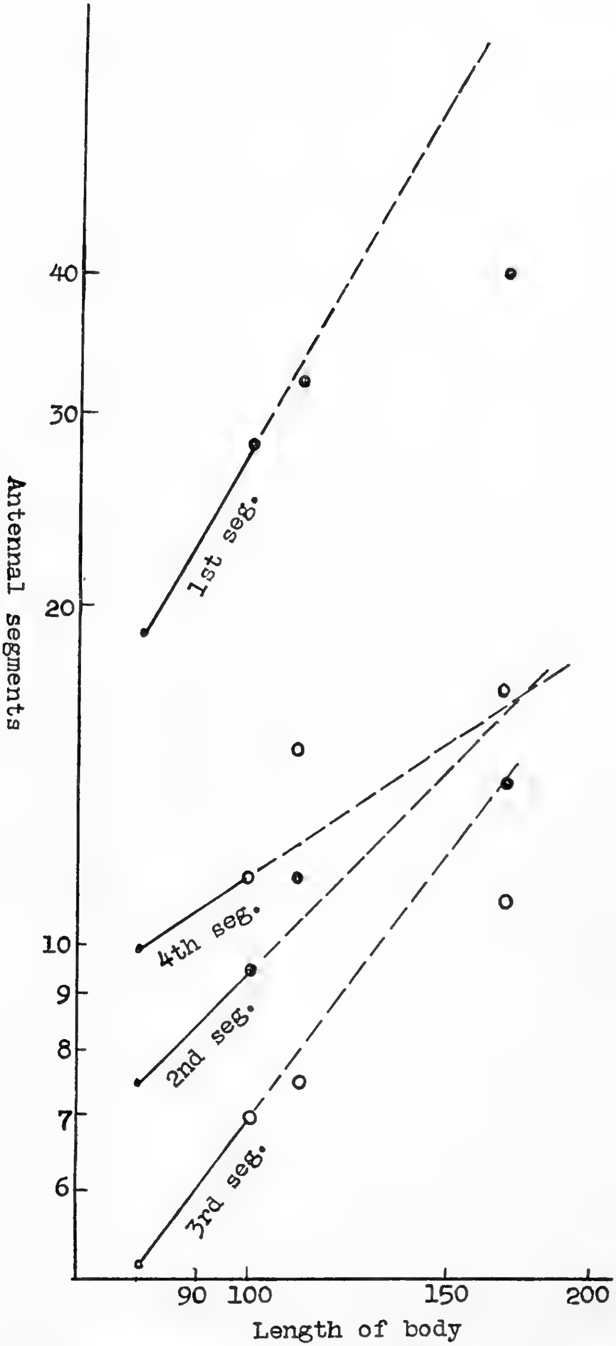
FIGURES 116, 117





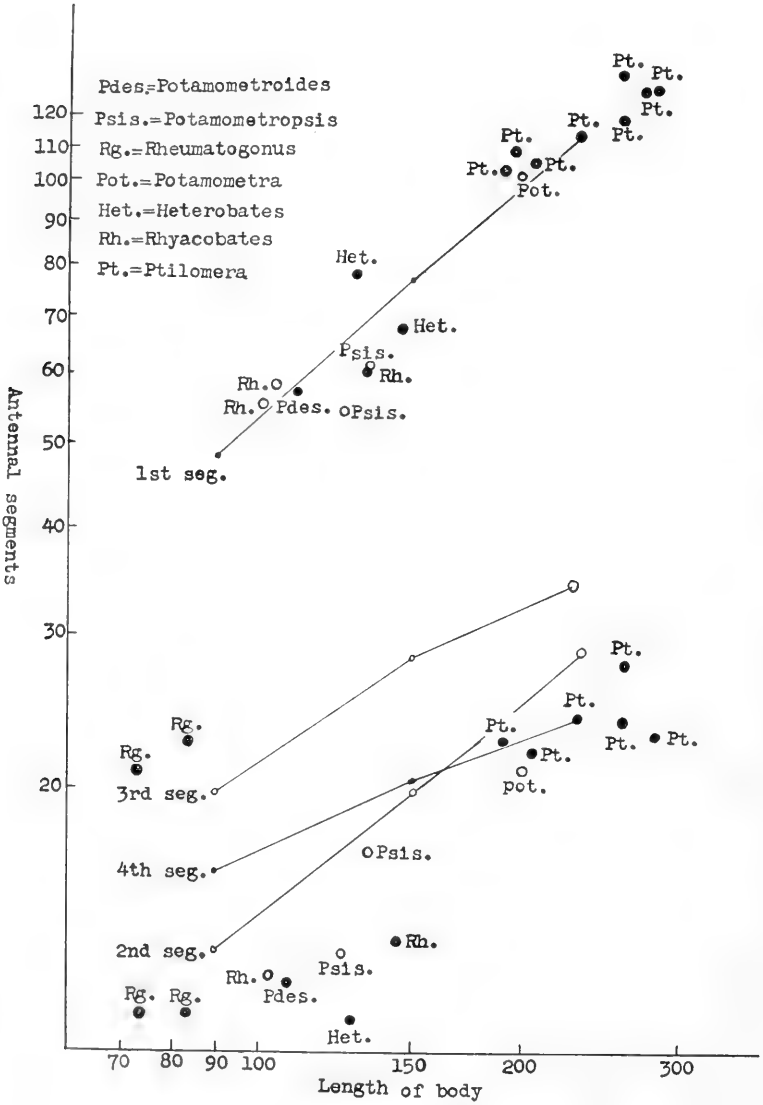
116. Antennal segments in *Cylindrostethus* from the Western Hemisphere.
117. First and fourth antennal segments in *Potamobates.*

FIGURE 118



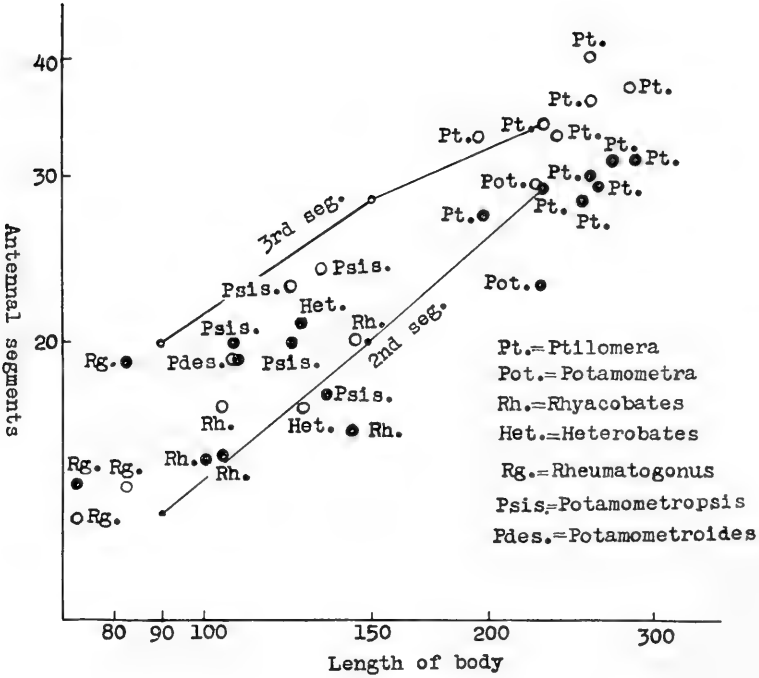
118. Antennal segments in *Platygerris*.

FIGURE 119



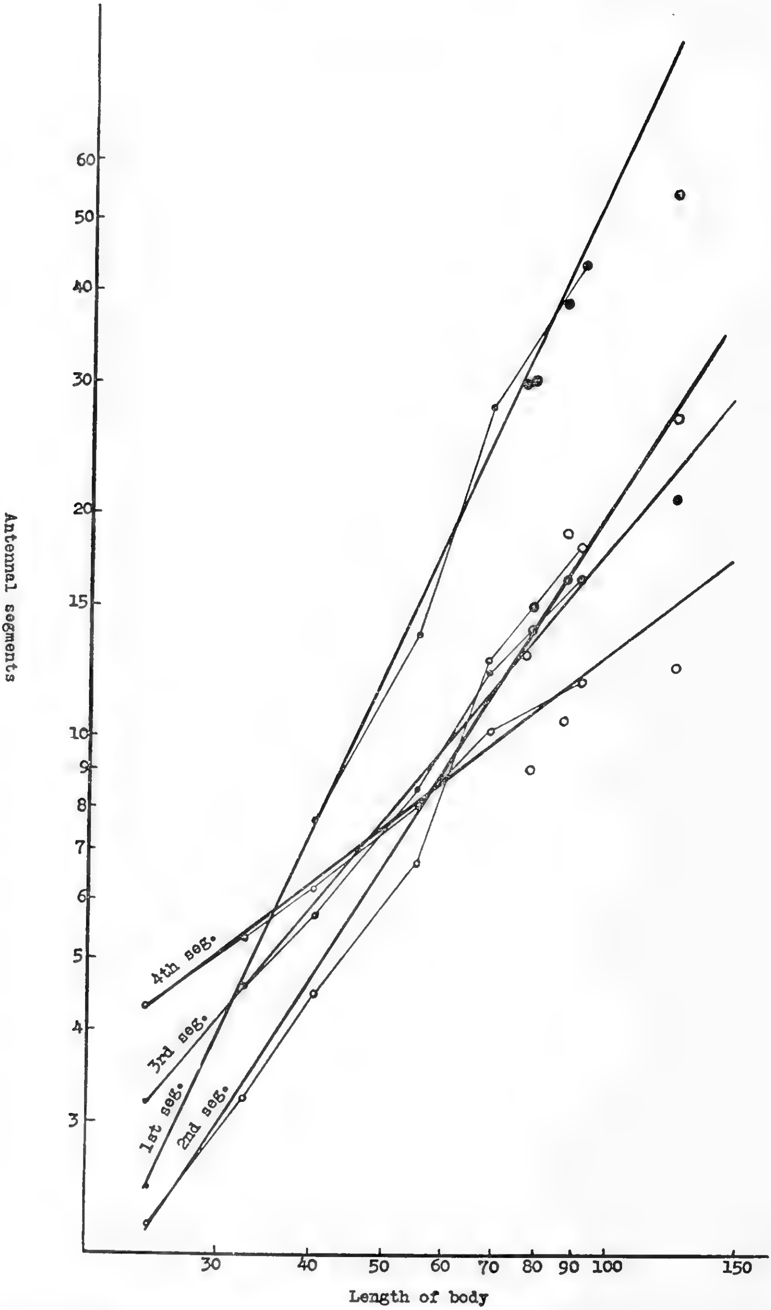
119. Antennal segments in *ptilomerinae.*

FIGURE 120



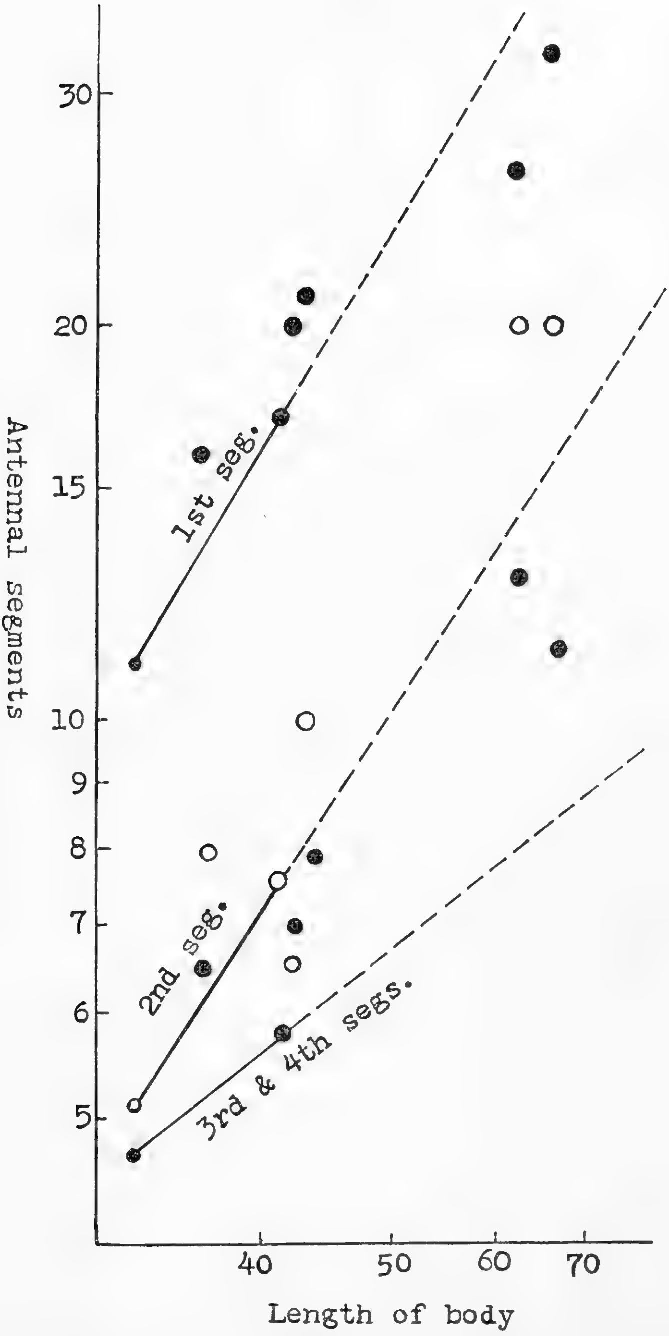
120. Second and third antennal segments in *ptilomerinae.*

FIGURE 121



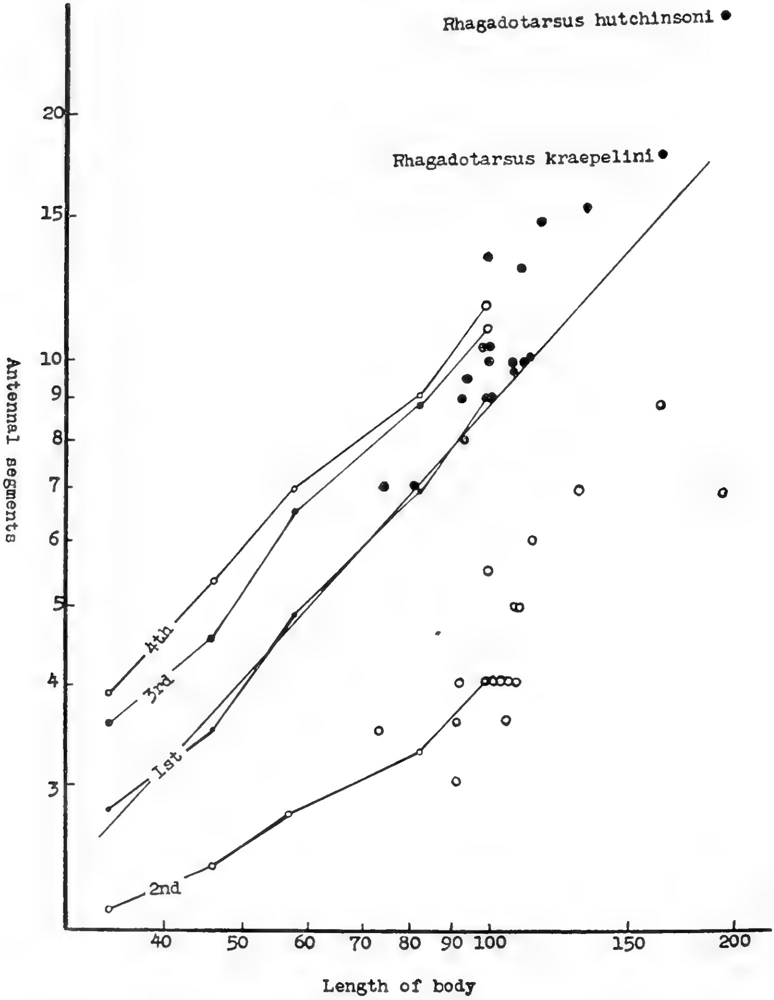
121. Antennal segments in *Metrocoris*. Each connected point is mean value at different stages.

FIGURE 122



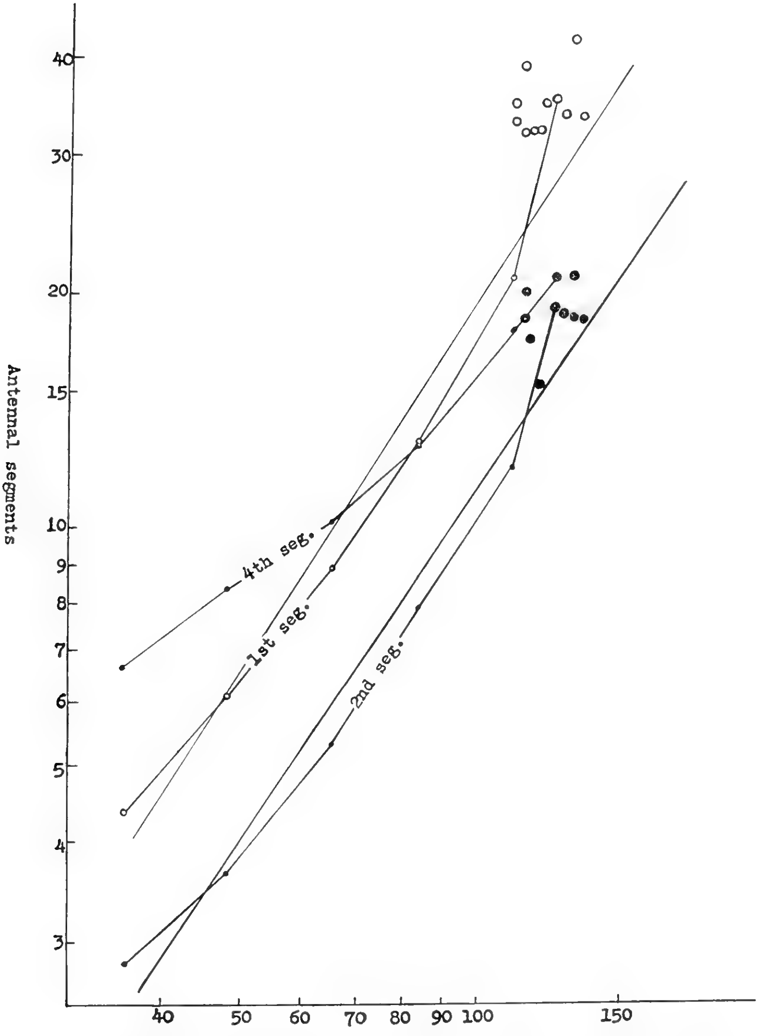
122. Antennal segments in *Ventidius*.

FIGURE 123



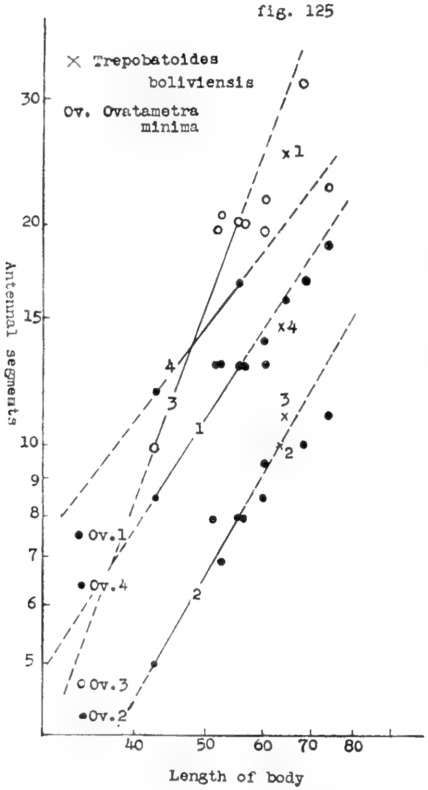
123. Antennal segments in *Rhagadotarsinae.* Each connected point is mean value at different stages (2 individuals at each stage).

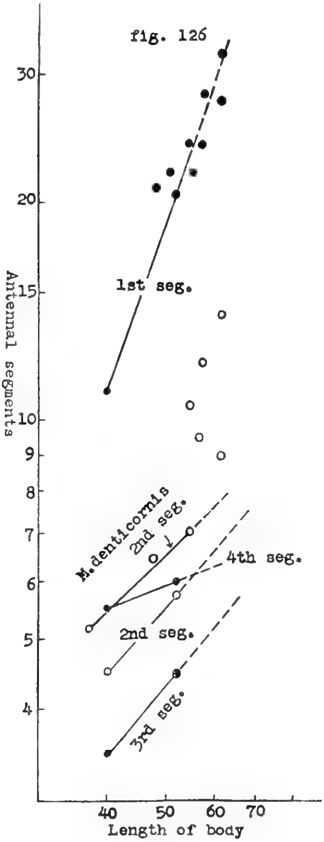
FIGURE 124



124. Antennal segments in *Trepobates*. Each connected point is mean value at different stages.

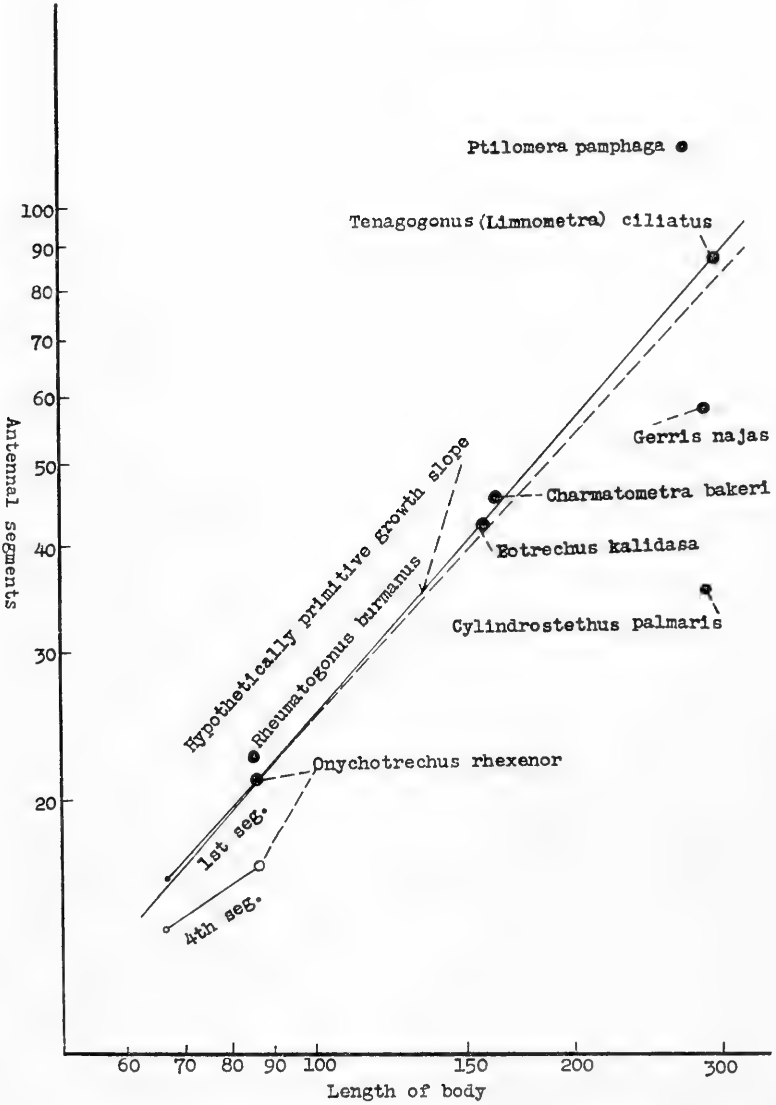
FIGURES 125, 126





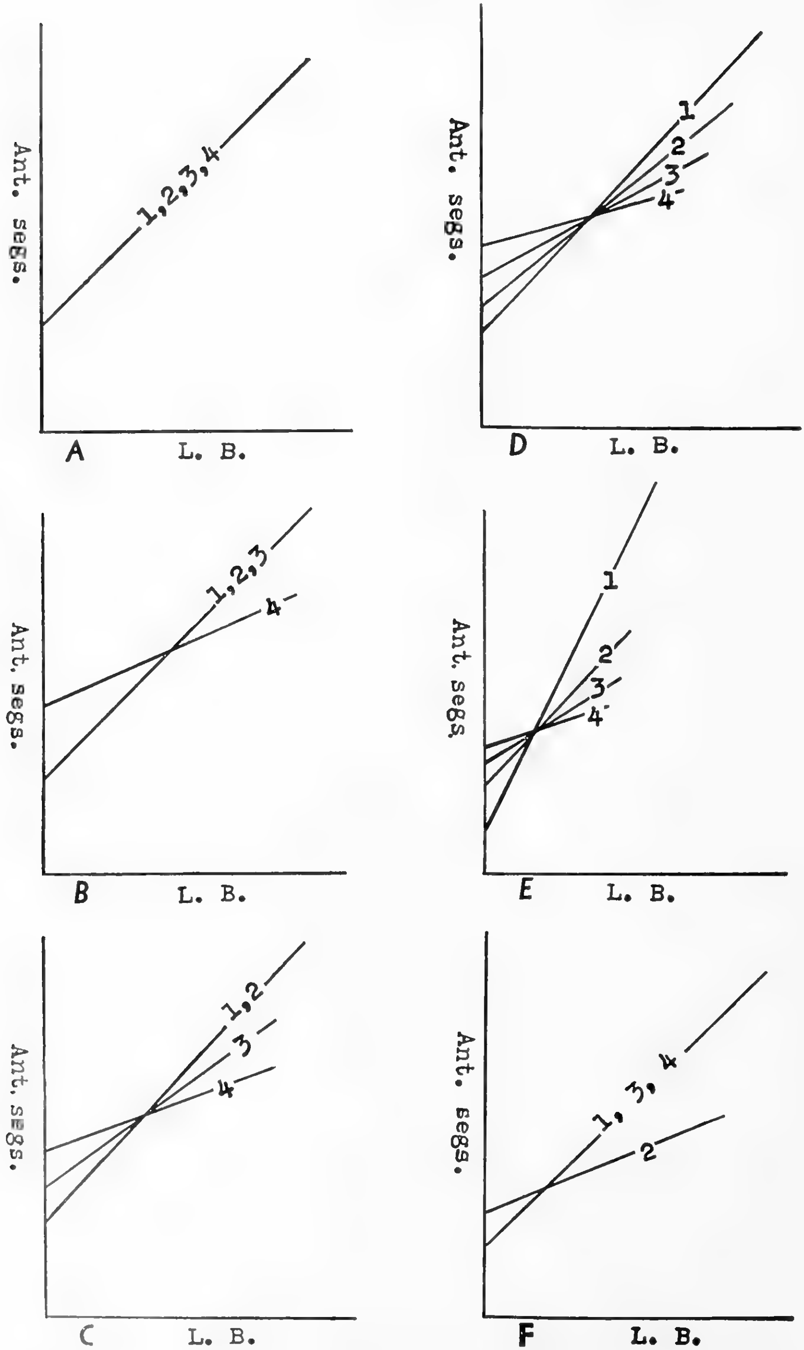
125. Antennal segments in *Telmatometra* and related genera.
126. Antennal segments in *Metrobates.*

Figure 127



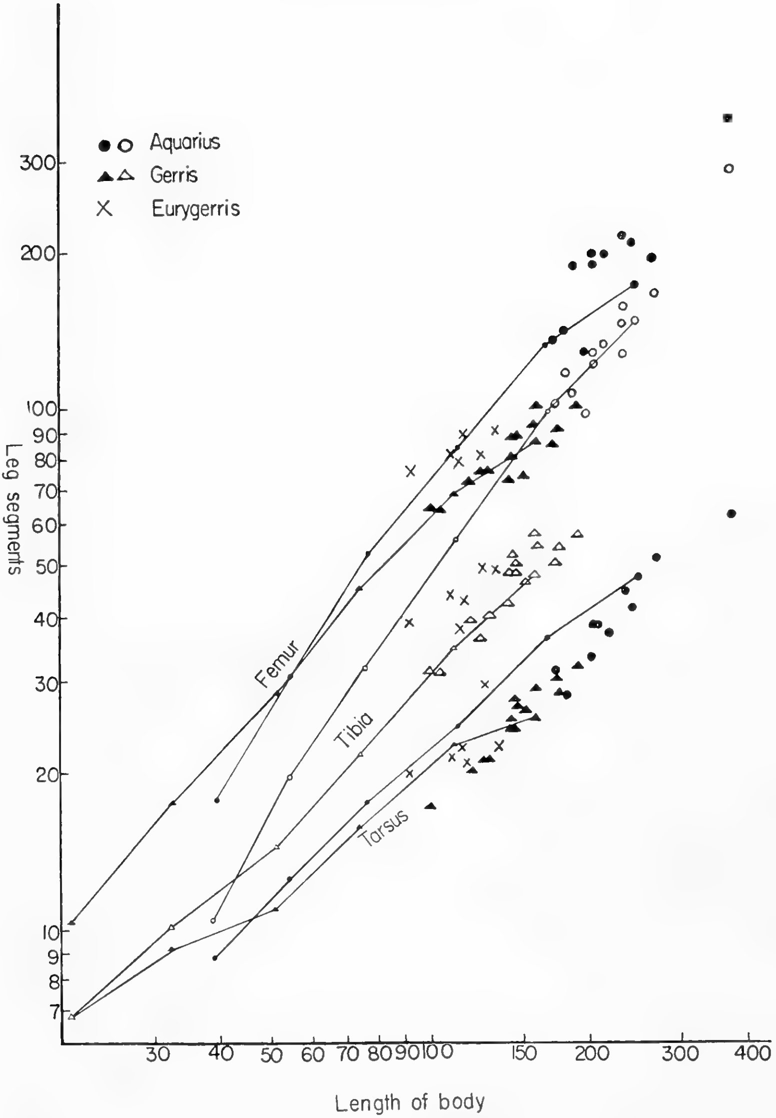
127. Hypothetically primitive growth line for the antennal segment in *Gerridae*.

FIGURE 128



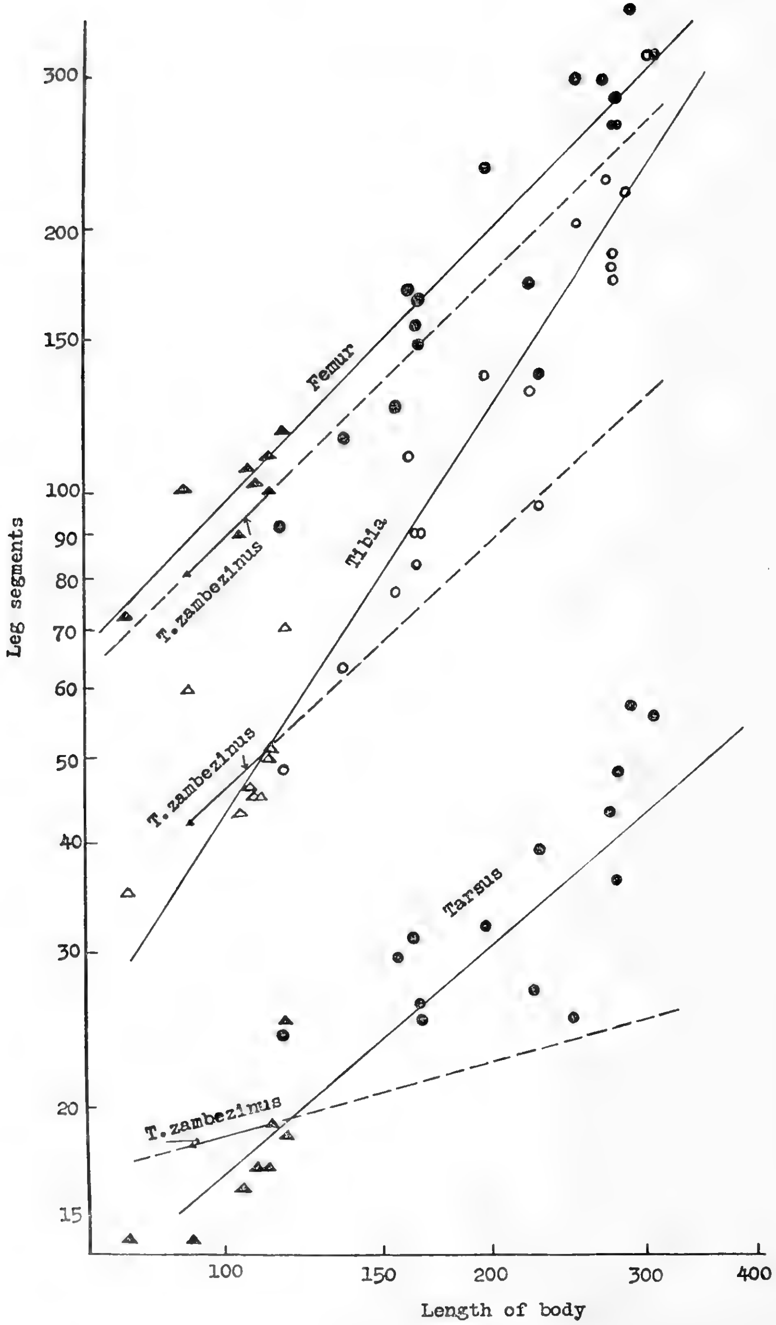
128. Diagram showing the evolution of growth gradient for antennal segments.

FIGURE 129



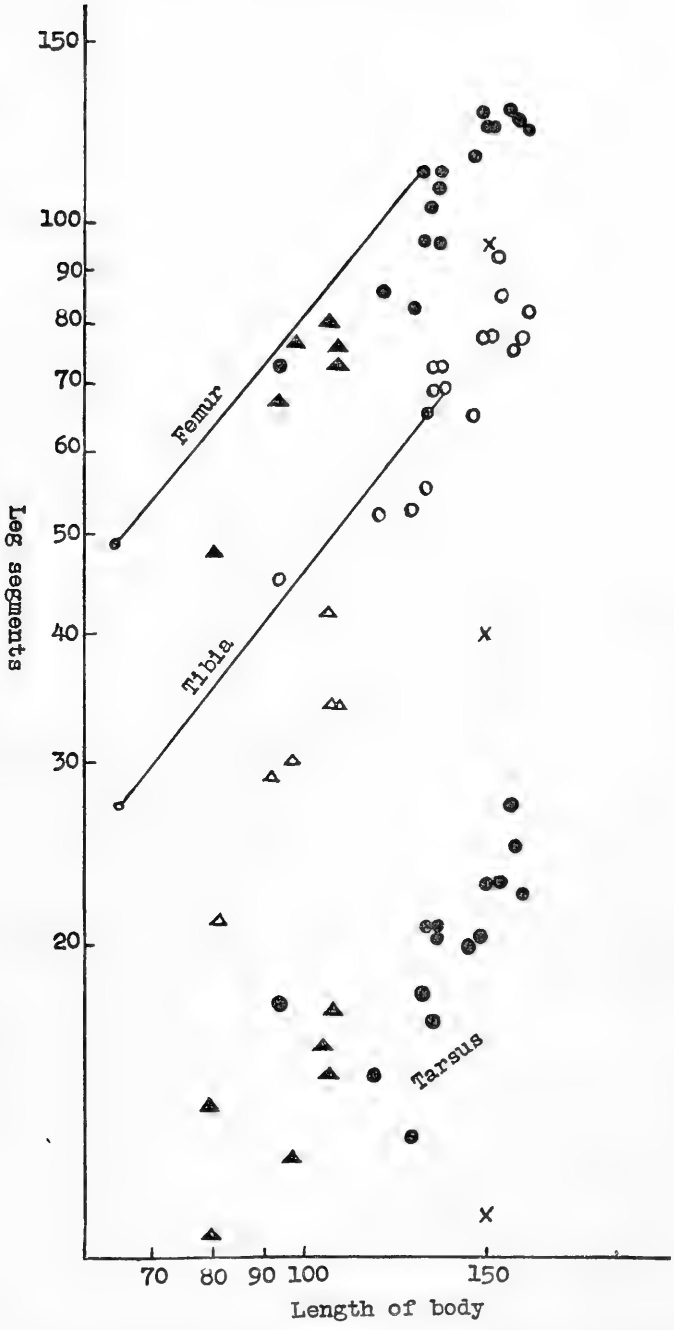
129. Hind leg segments in *Gerris*. Each connected point is mean value at different stages.

FIGURE 130



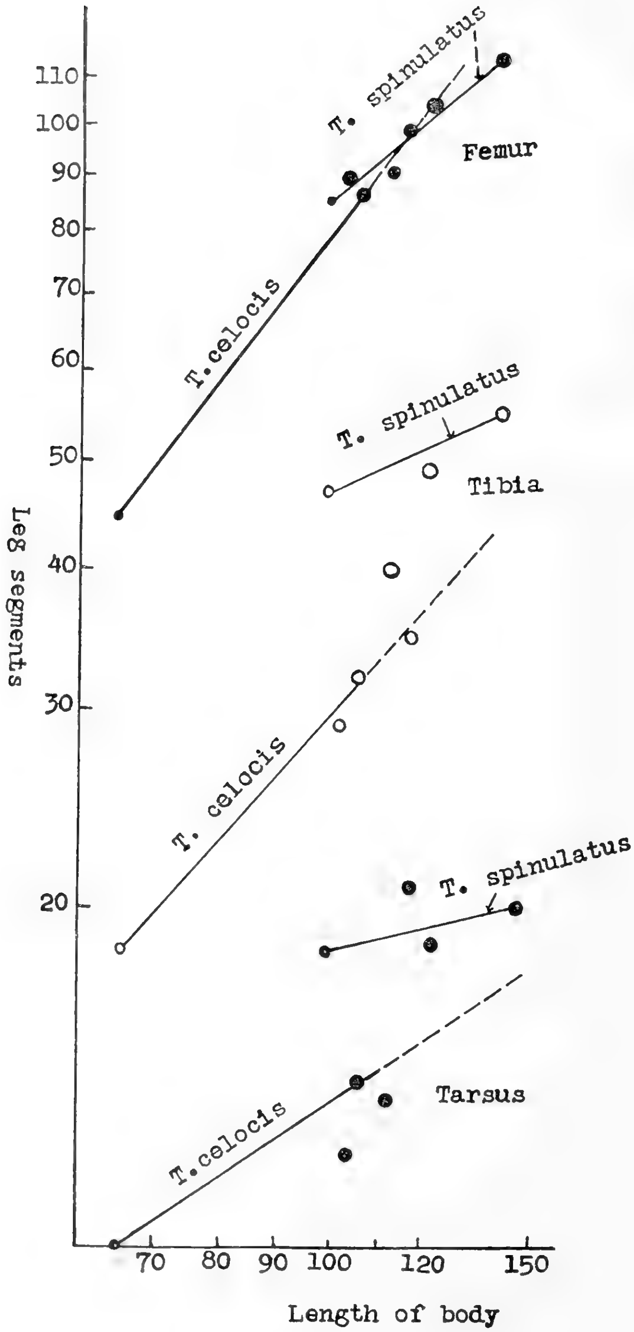
130. Hind leg segments in the *Limnometra-Tenagogonus s. str.* complex. Round points are *Limnometra,* triangles represent *Tenagogonus s. str.*

FIGURE 131



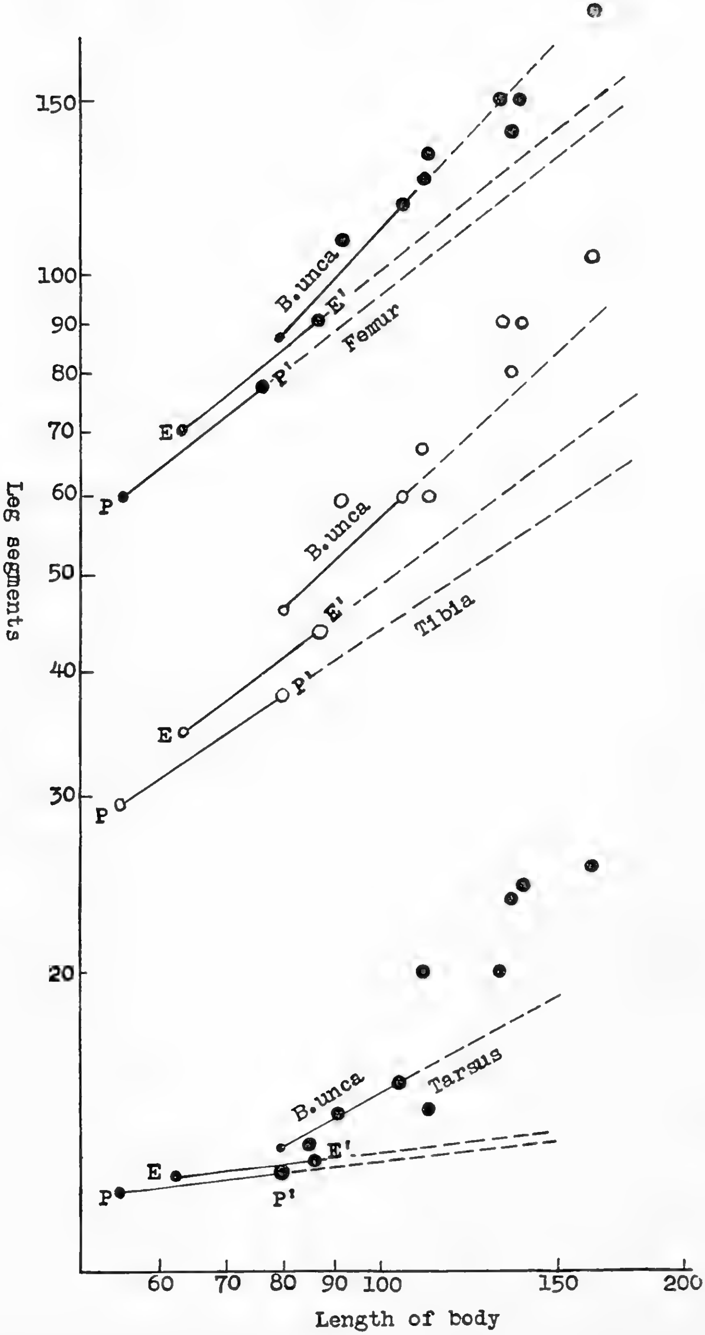
131. Hind leg segments in *Limnogonus.* Round points are *Limnogonus s. str.* triangle points represent *Limnogonellus.*

FIGURE 132



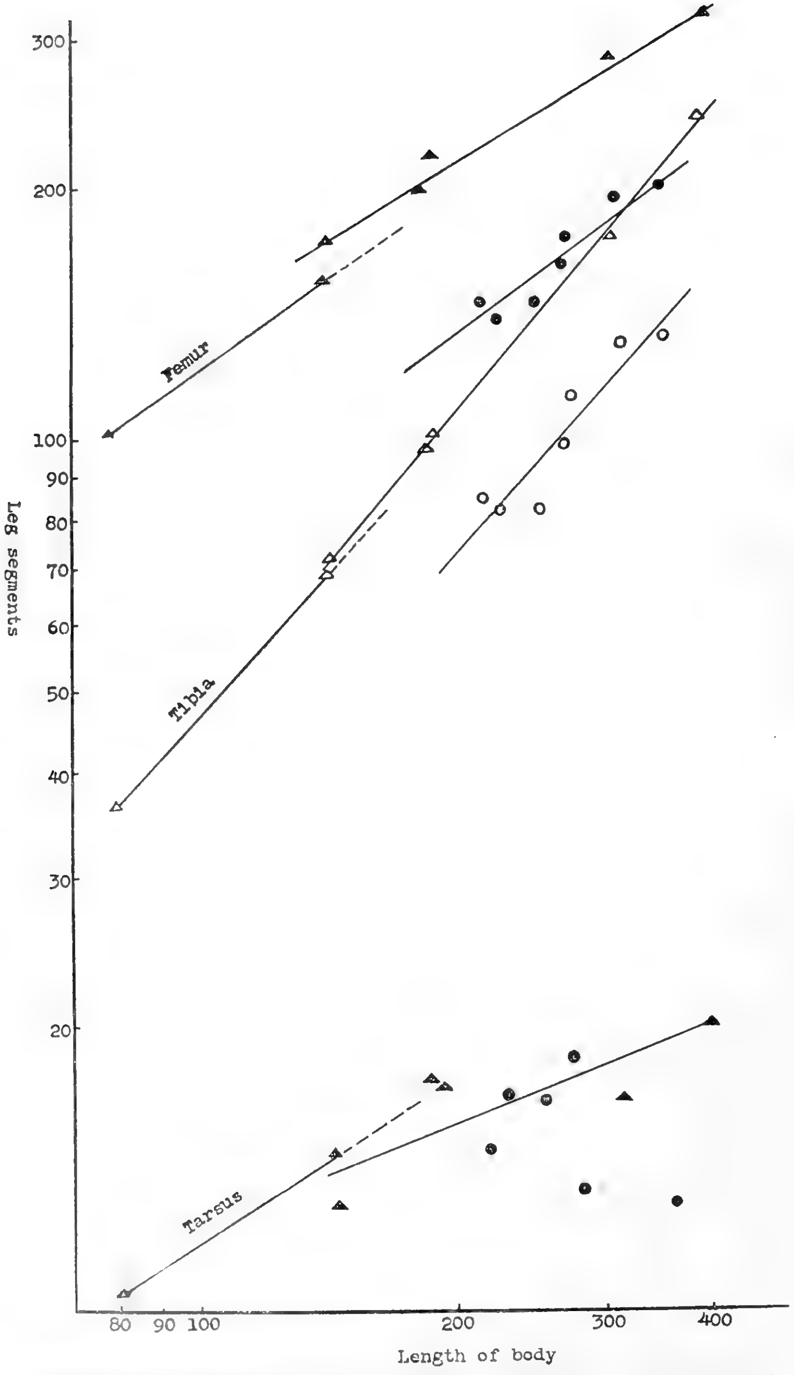
132. Hind leg segments in *Tachygerris*.

FIGURE 133



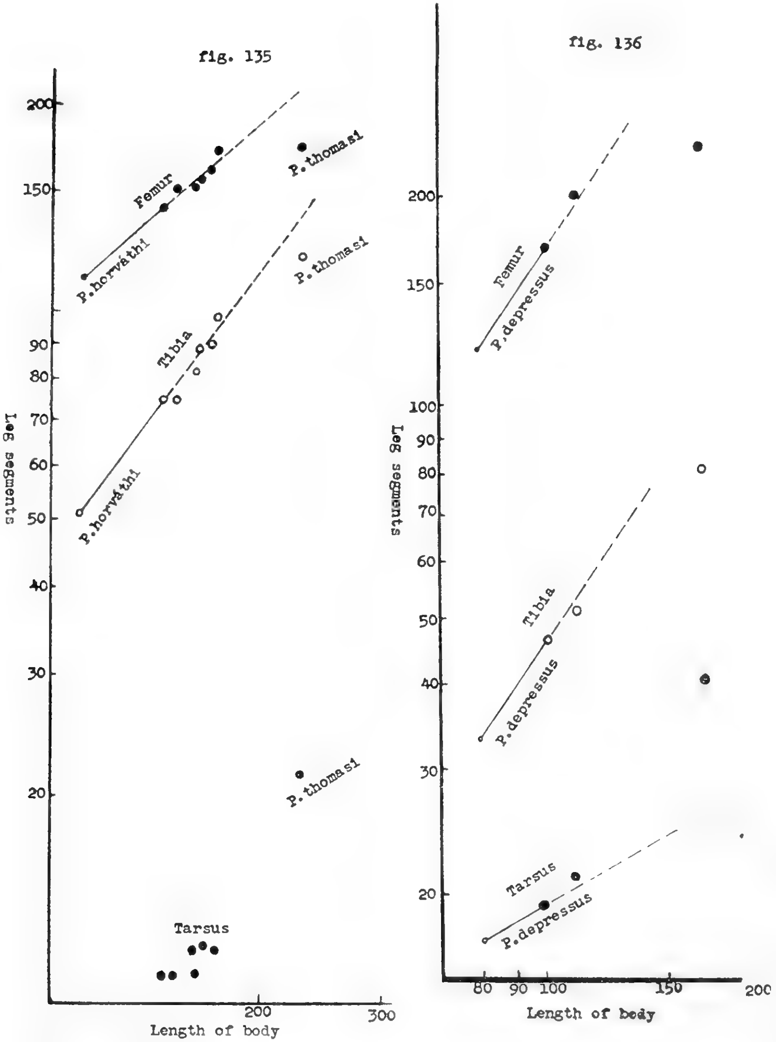
133. Hind leg segments in Charmatometrini. E E′ are for a species from Ecuador; p p′ are for a species from Panama.

FIGURE 134



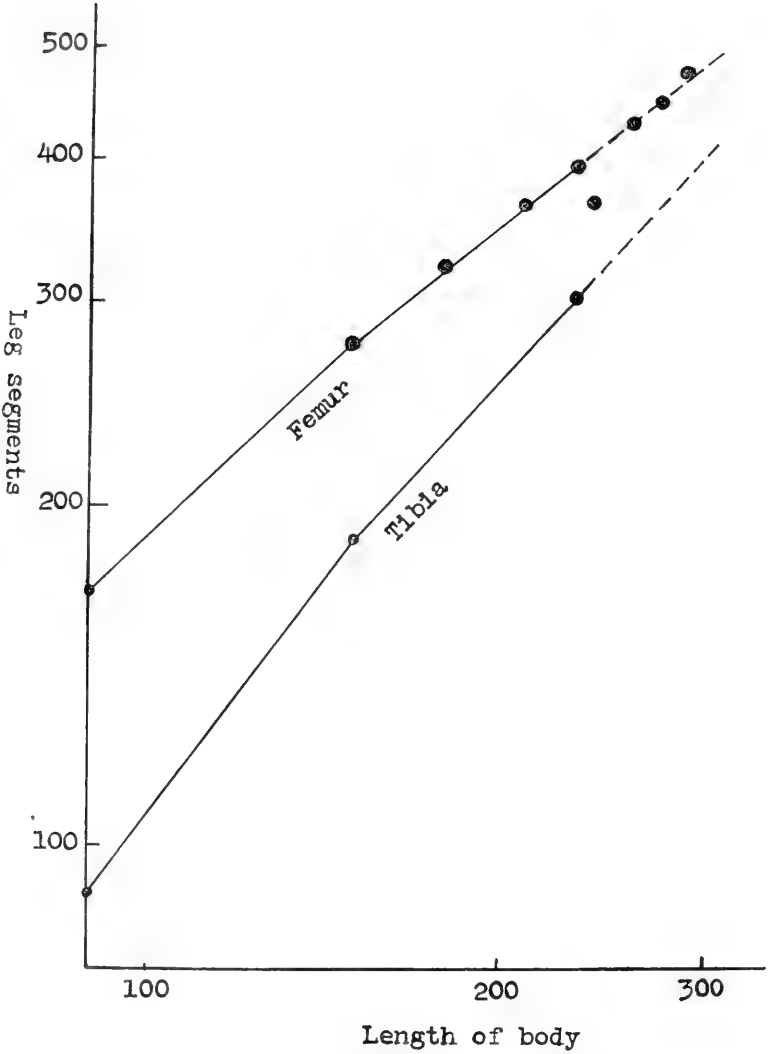
134. Hind leg segments in *Cylindrostethus.* Triangles for species from the Eastern Hemisphere: round spots for the species from the Western Hemisphere.

FIGURES 135, 136



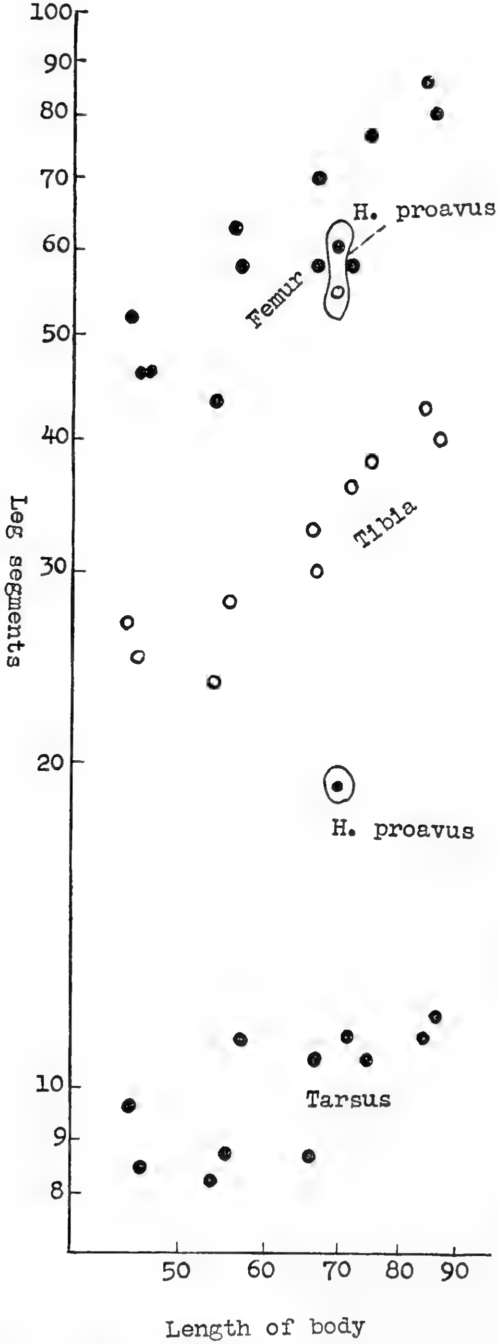
135. Hind leg segments in *Potamobates*.
136. Hind leg segments in *Platygerris*.

FIGURE 137



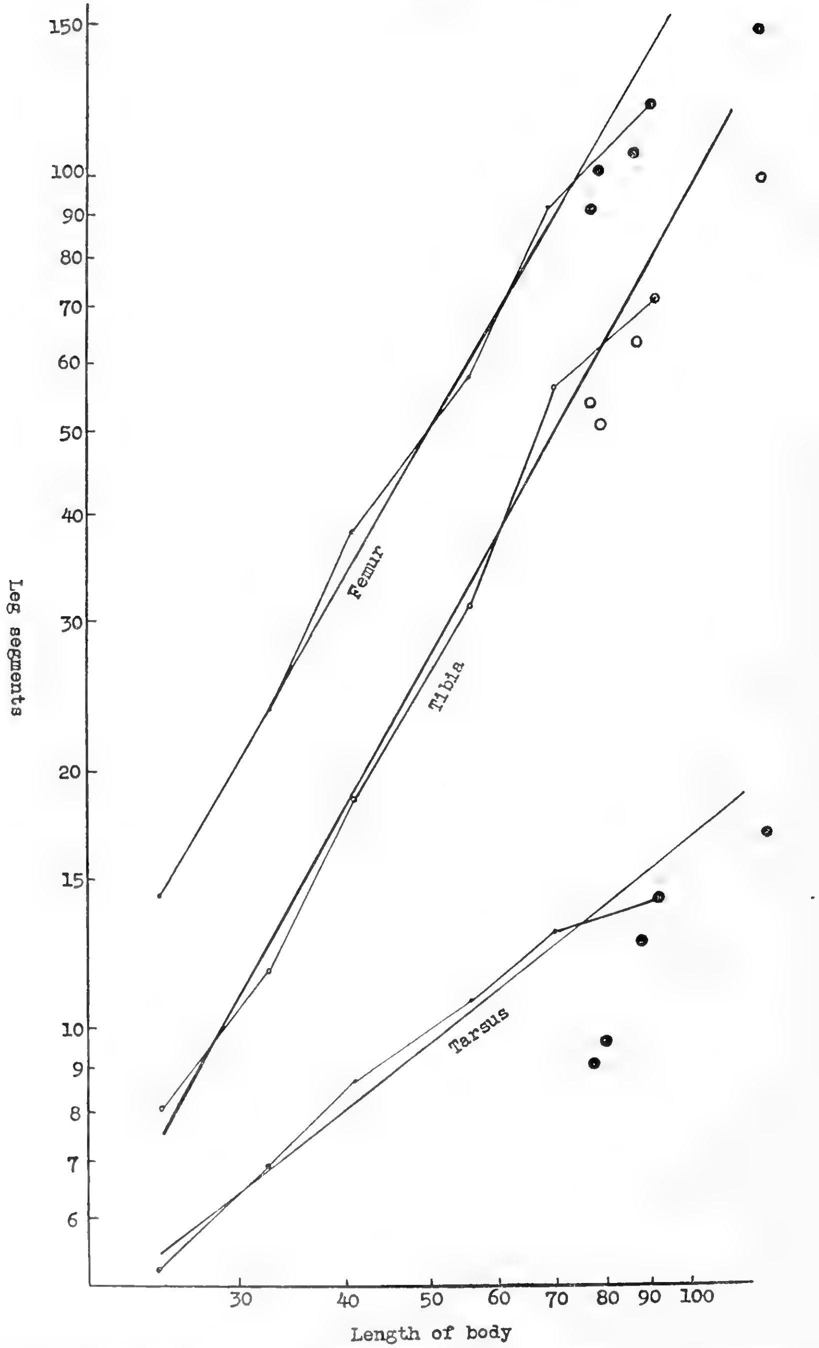
137. Hind leg segments in *Ptilomera*.

FIGURE 138



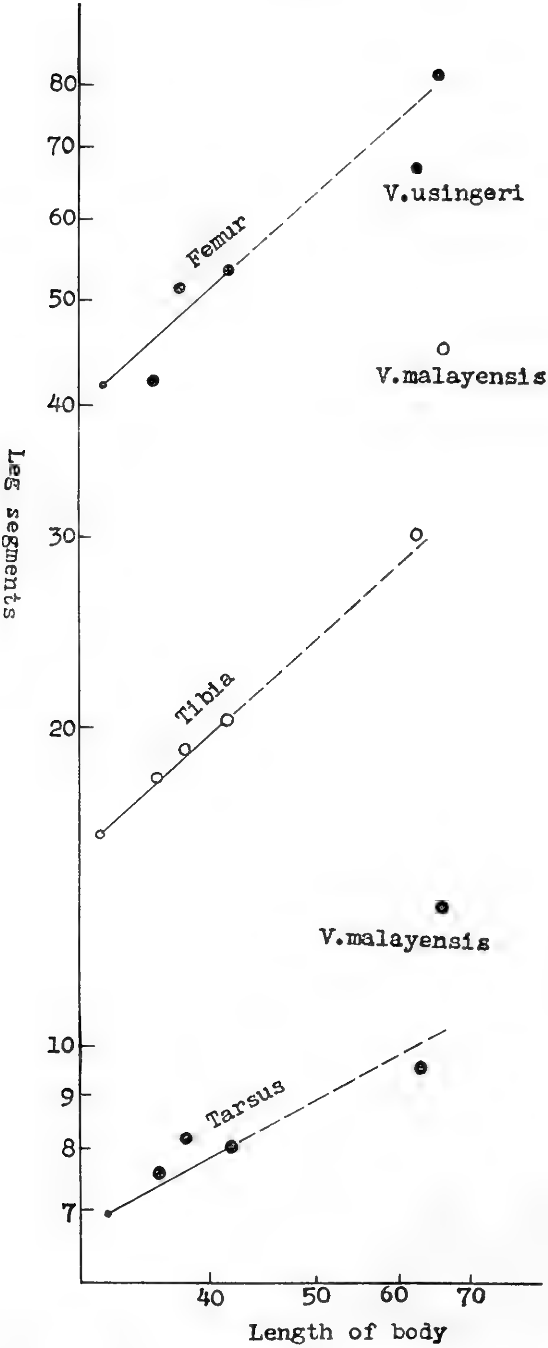
138. Hind leg segments in *Halobatini.*

FIGURE 139



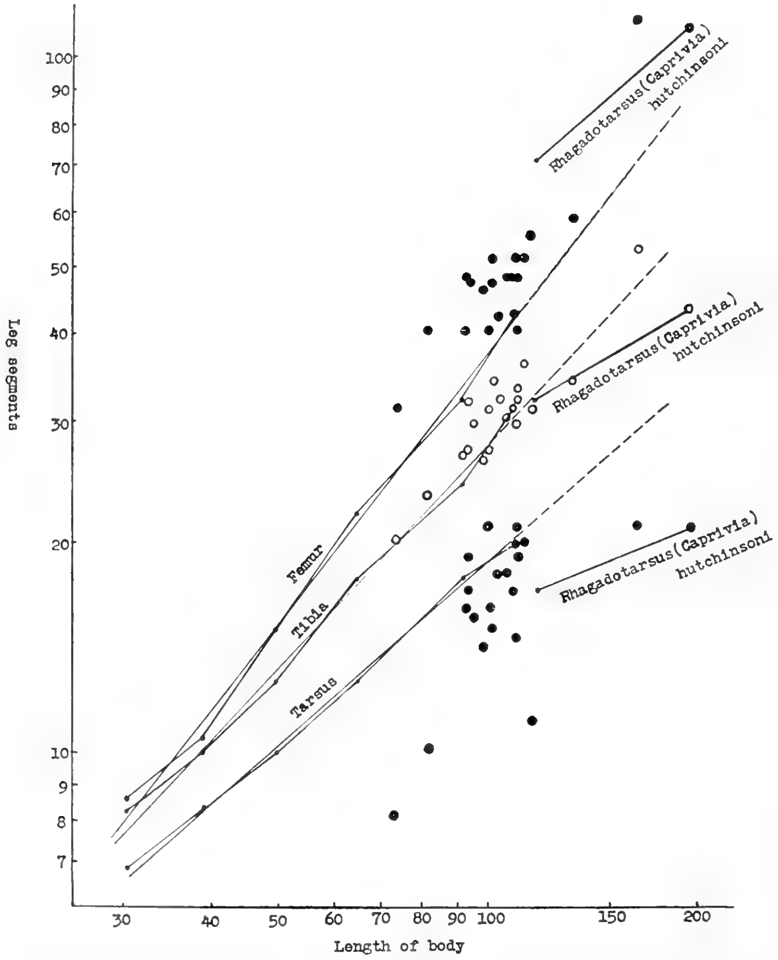
139. Hind leg segments in *Metrocoris*. Each connected point represents mean value at different stages.

FIGURE 140



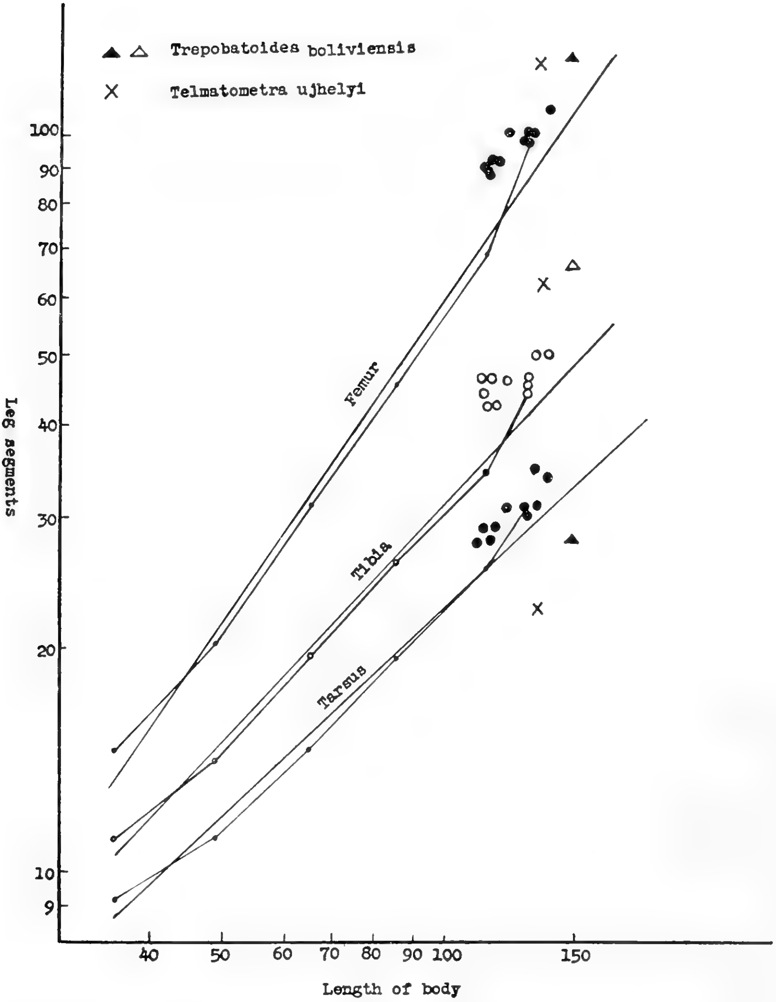
140. Hind leg segments in *Ventidius*. Growth line is for *V. henryi*.

FIGURE 141



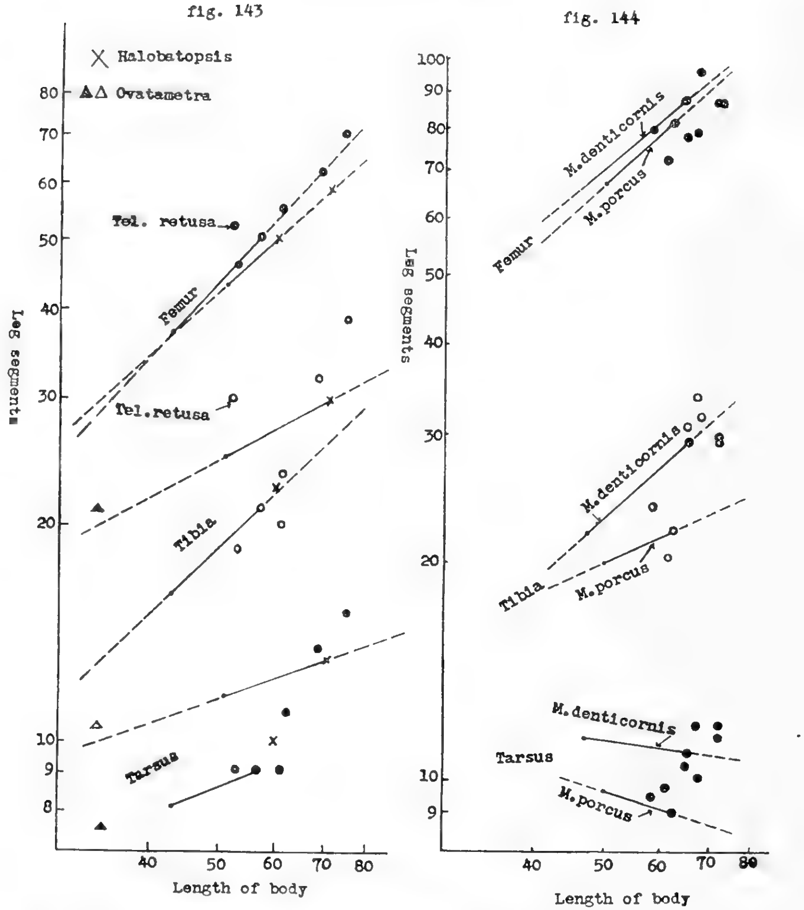
141. Hind leg segments in Rhagadotarsinae. Each connected point represents mean value at different stages.

Figure 142



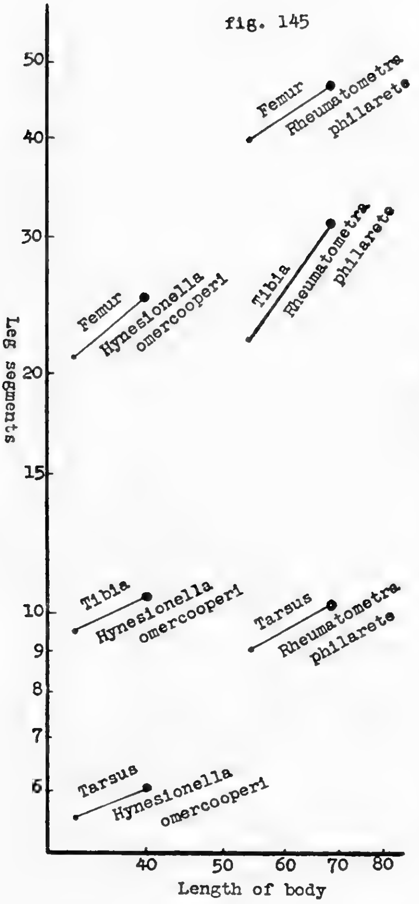
142. Hind leg segments in *Trepobates* and related genera. Each connected point represents mean value at different stages.

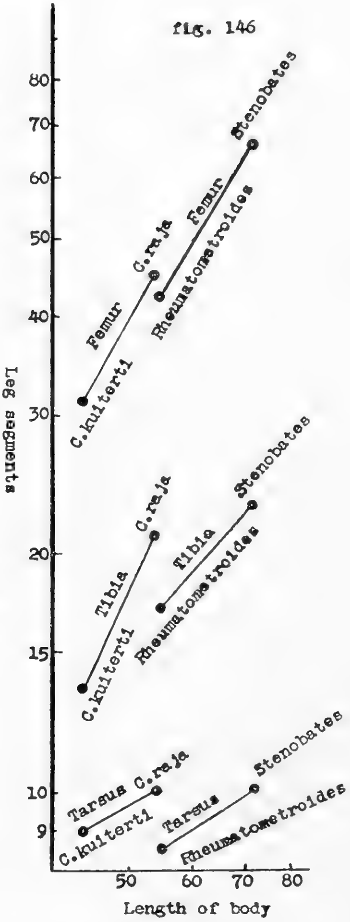
FIGURES 143, 144



143. Hind leg segments in *Telmatometra* and related genera.
144. Hind leg segments in *Metrobates*.

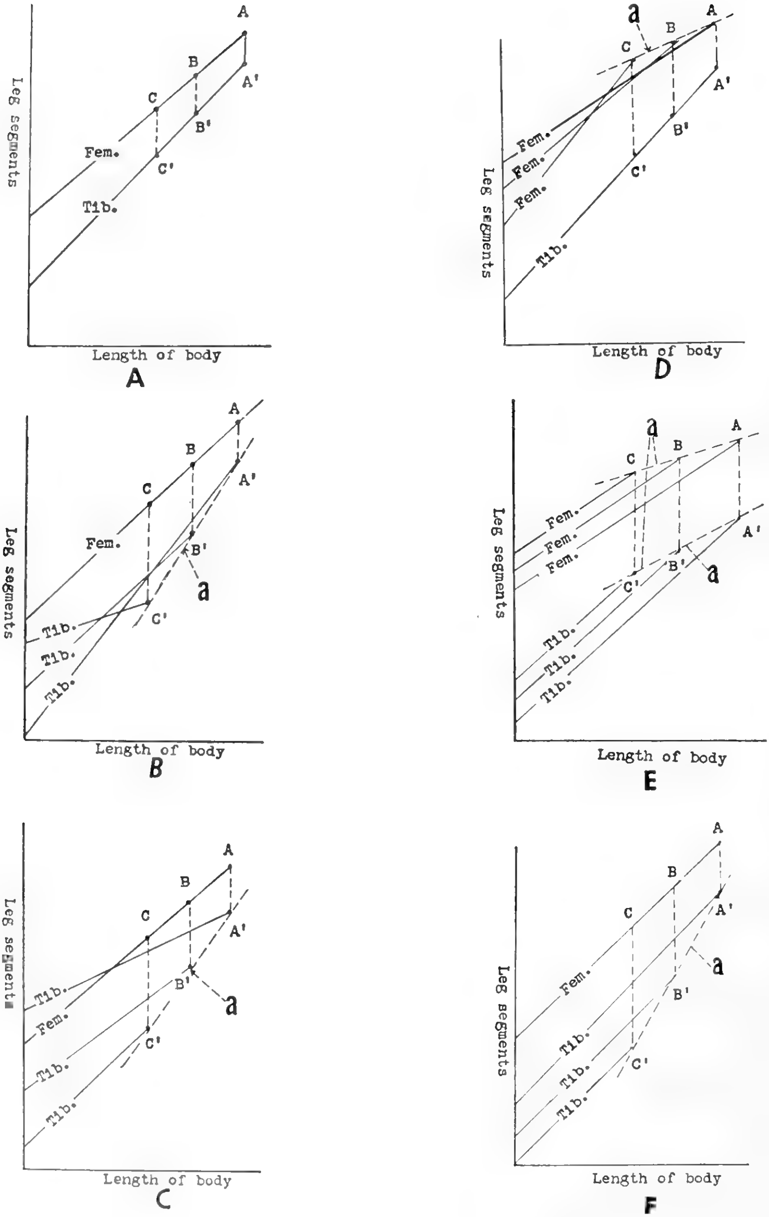
FIGURES 145, 146





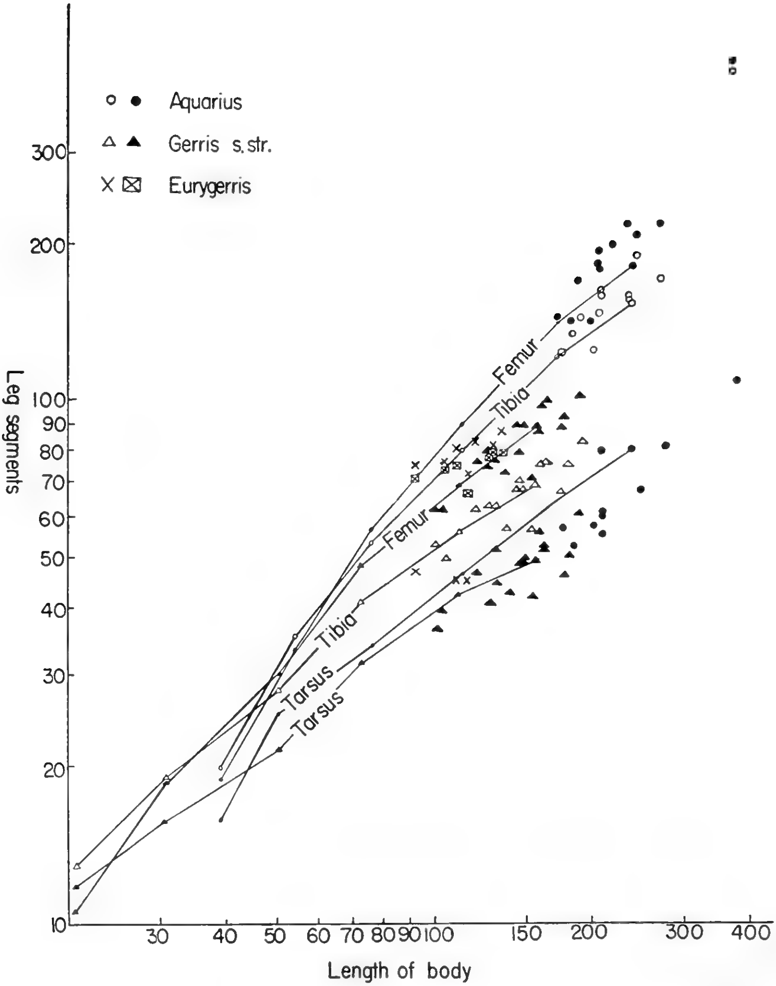
145. Hind leg segments in *Hynesionella* and *Rheumatometra.*
146. Hind leg segments in *Cryptobates* and *Rheumatometroides.*

FIGURE 147



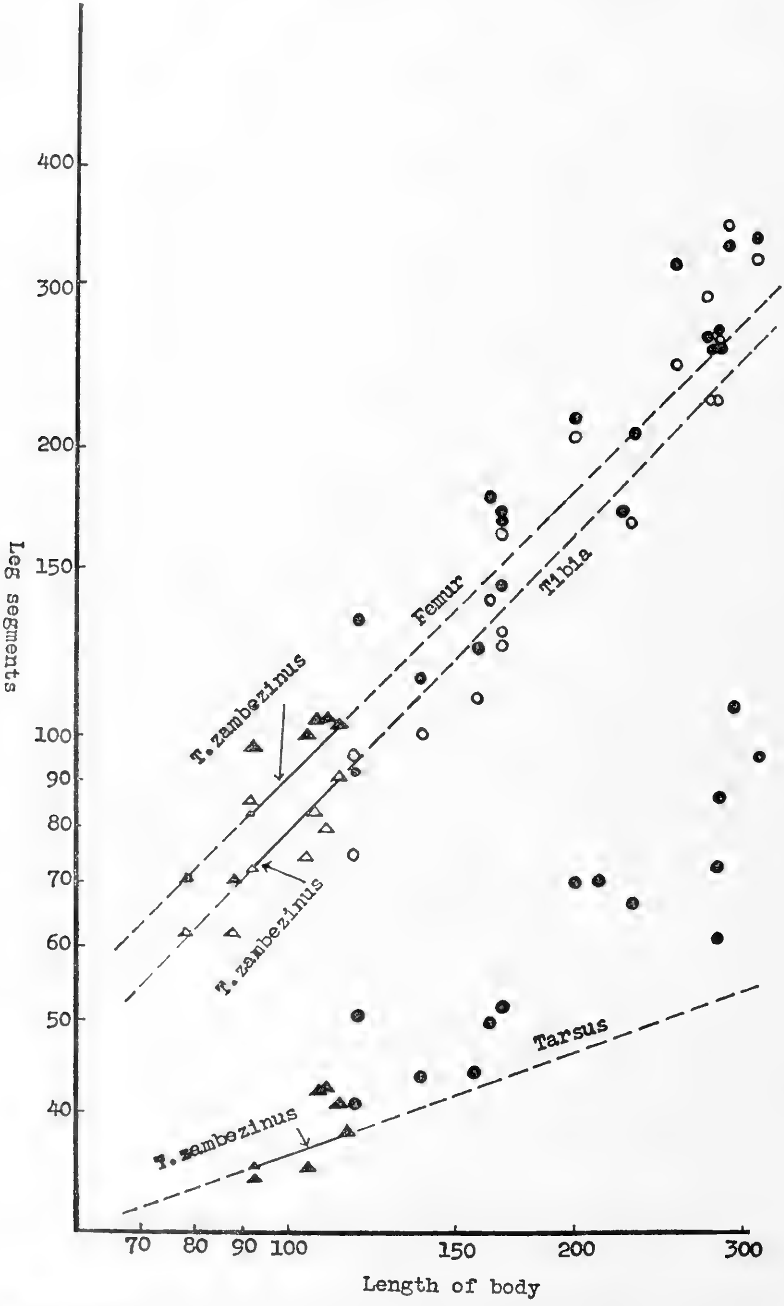
147. Evolution of hind leg segments (femur and tibia) in Gerridae, a is allomorphic line.

FIGURE 148



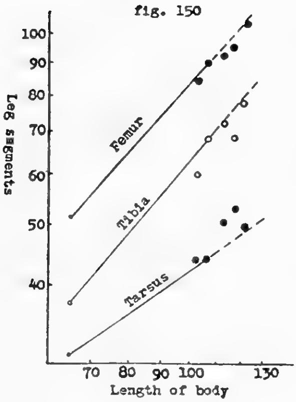
148. Middle leg segments in *Gerris*. Each connected point represents mean value at different stages.

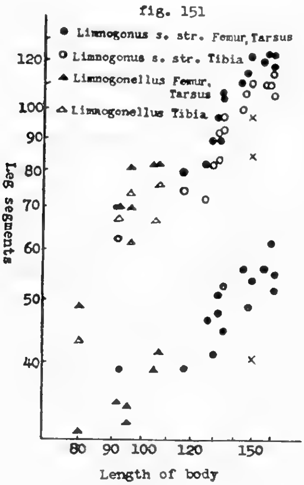
FIGURE 149

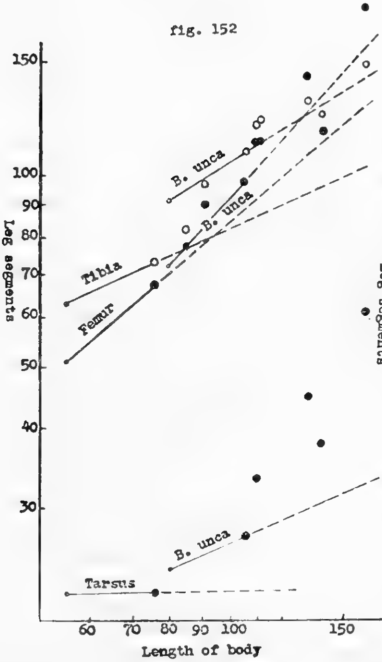


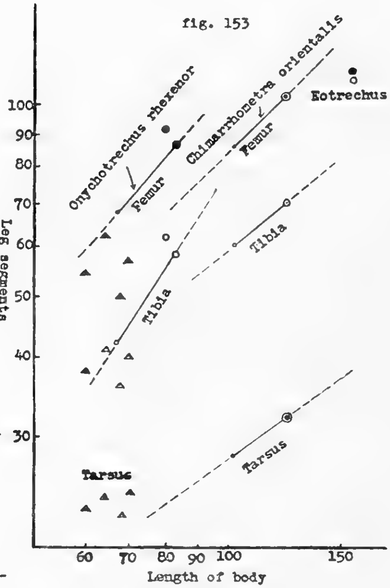
149. Middle leg segments in the *Limnometra-Tenagogonus s. str.* complex.

FIGURES 150-153









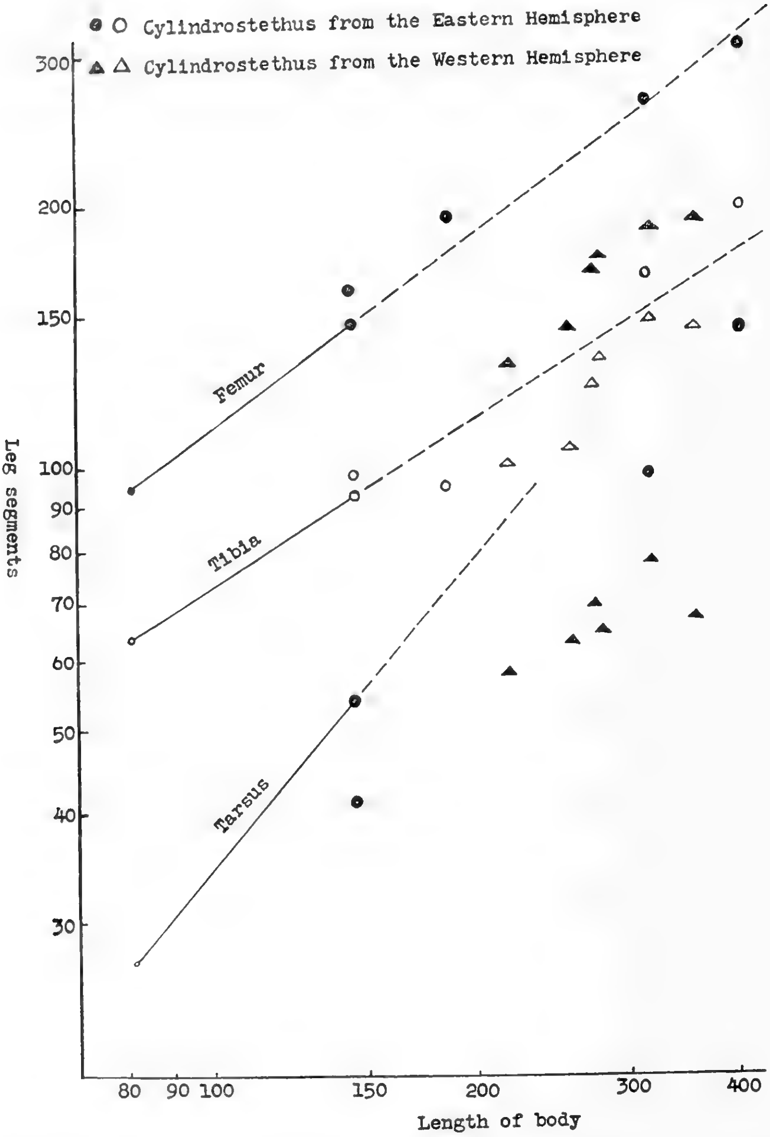
150. Middle leg segments in *Tachygerris*.

151. Middle leg segments in *Limnogonus s. str.-Limnogonellus* complex. Round points for *Limnogonus s. str.*, triangle points for *Limnogonellus*. White points for tibiae.

152. Middle leg segments in Charmatometrini.

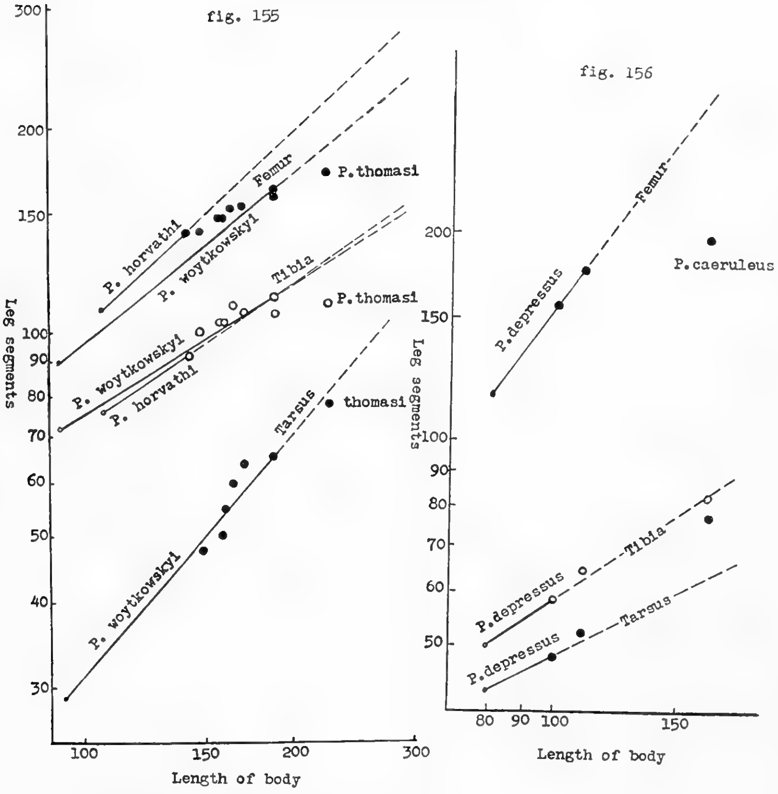
153. Middle leg segments in Eotrechini.

FIGURE 154



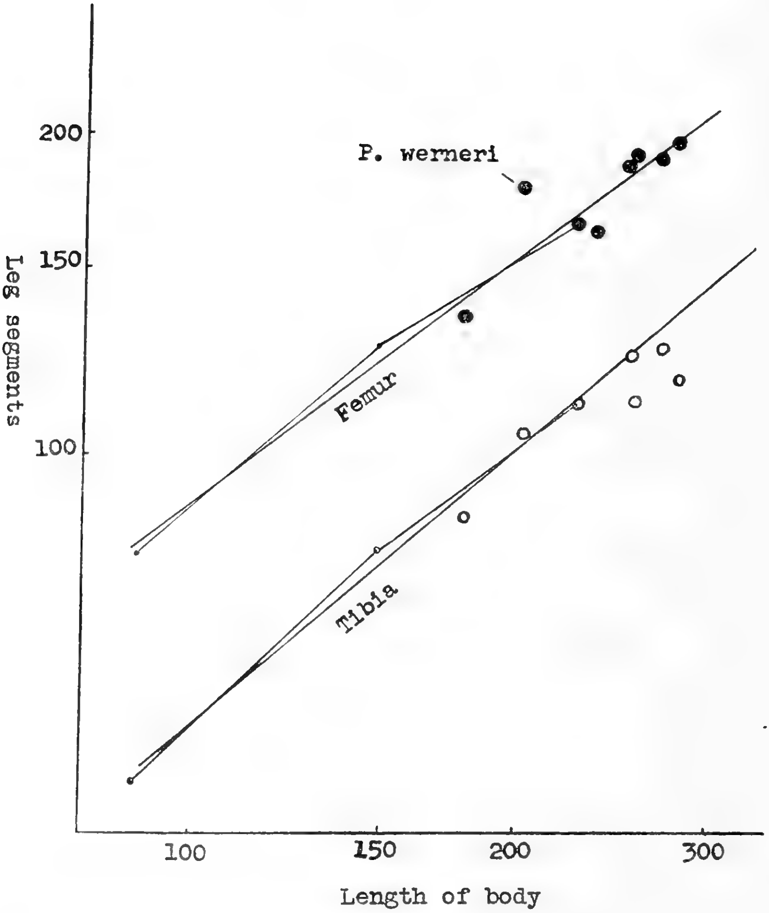
154. Middle leg segments in *Cylindrostethus.* Round points for species from Eastern Hemisphere; triangle points for species from Western Hemisphere. *Cylindrostethus sumatranus* Lundblad is not plotted.

FIGURES 155, 156



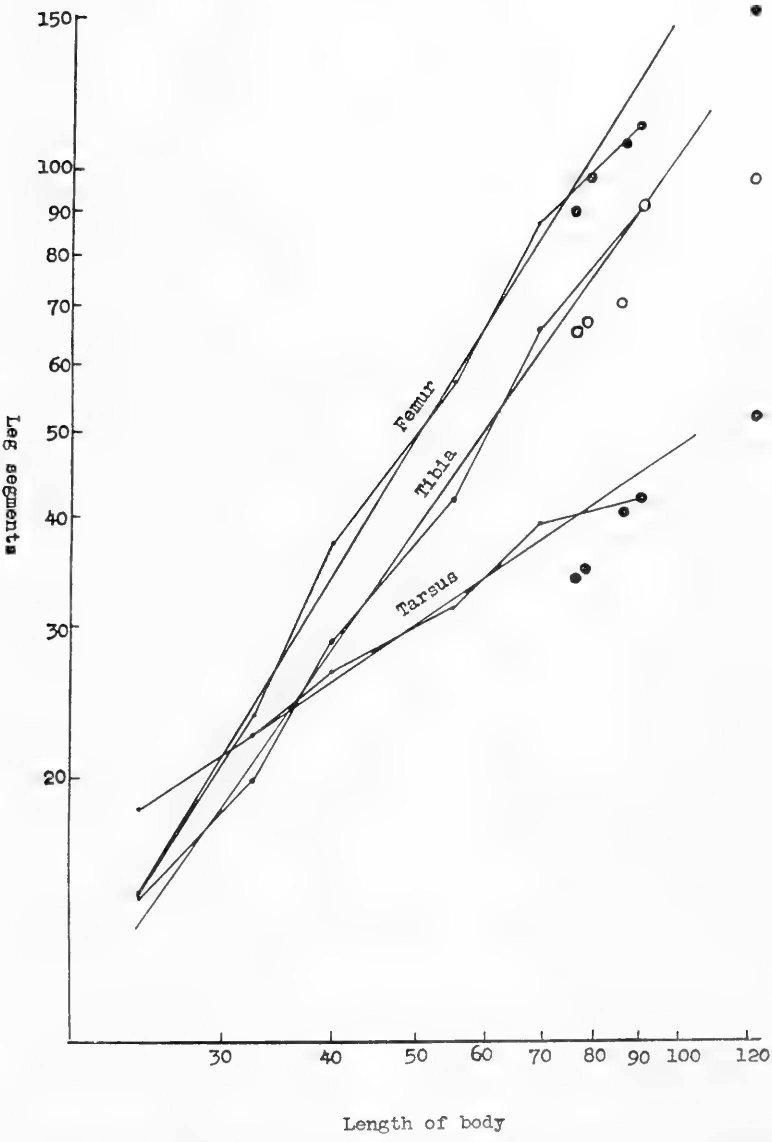
155. Middle leg segments of *Potamobates.*
156. Middle leg segments of *platygerris.*

FIGURE 157



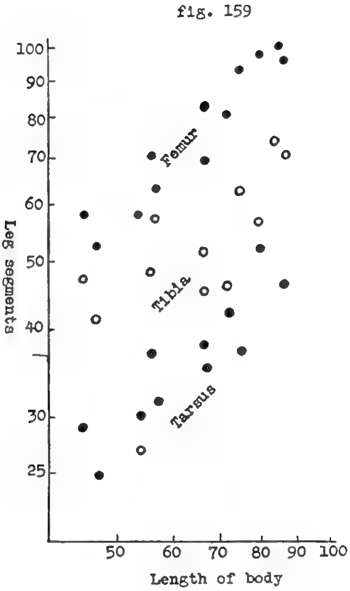
157. Middle leg segments in *Ptilomera.*

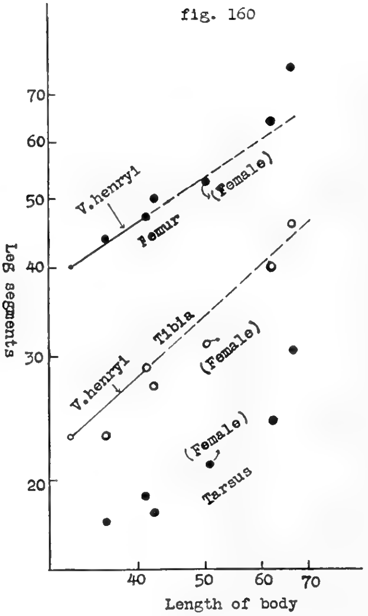
Figure 158



158. Middle leg segments in *Metrocoris*. Each connected point represents mean value at different stages.

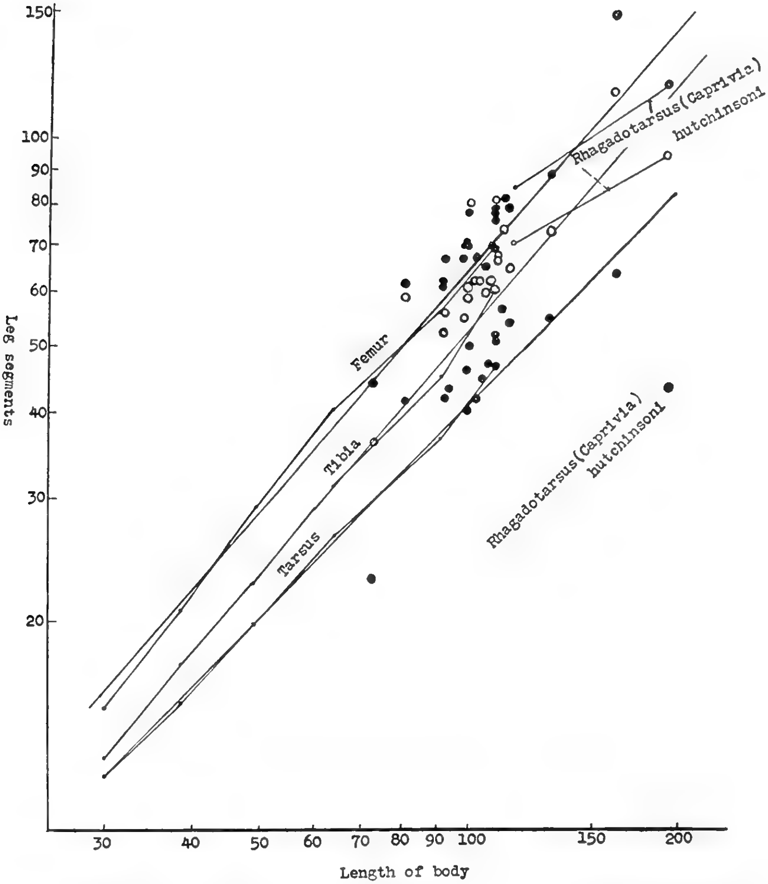
FIGURES 159, 160





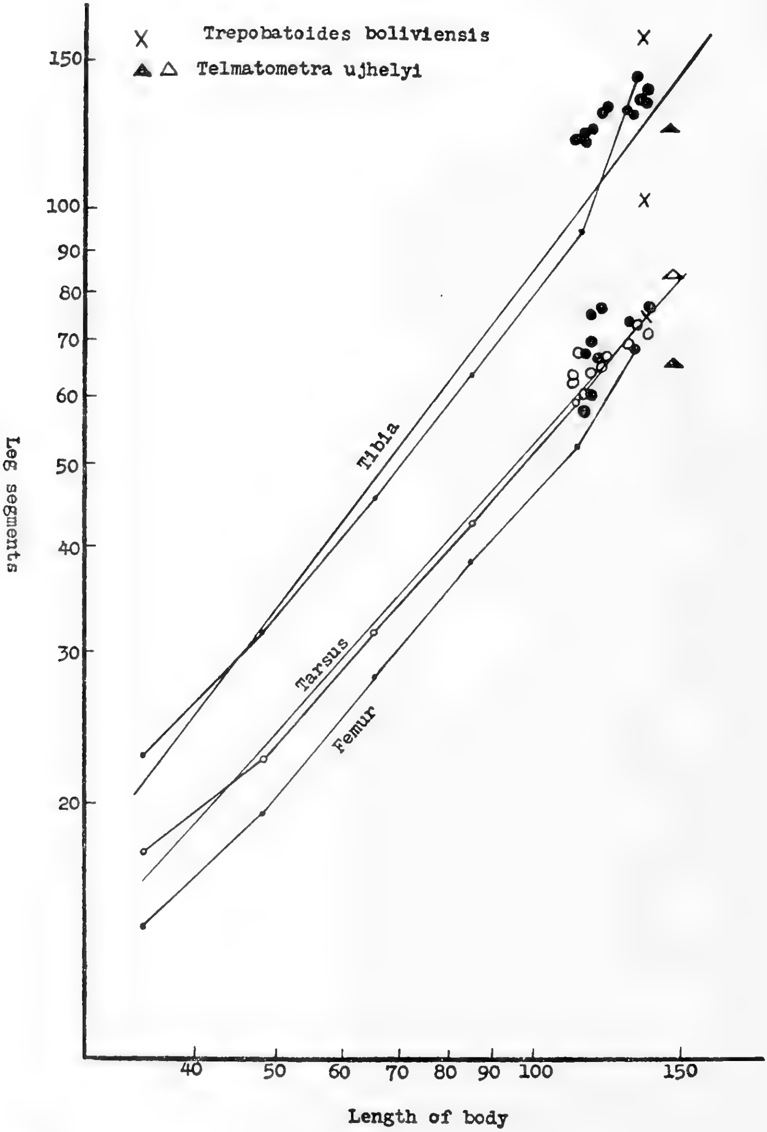
159. Middle leg segments in Halobatini.
160. Middle leg segments in *Ventidius.*

Figure 161



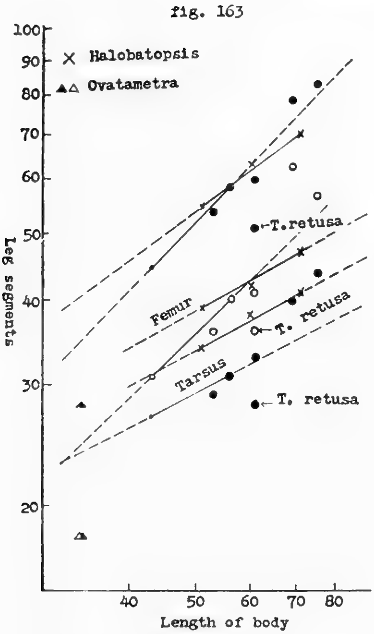
161. Middle leg segments in Rhagadotarsinae. Each connected point represents mean value at different stages.

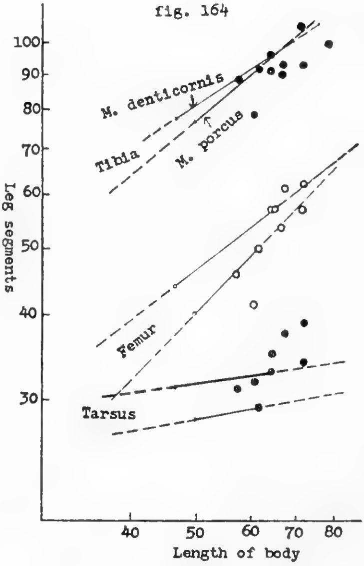
FIGURE 162



162. Middle leg segments in *Trepobates* and related genera. Each connected point represents mean value at different stages.

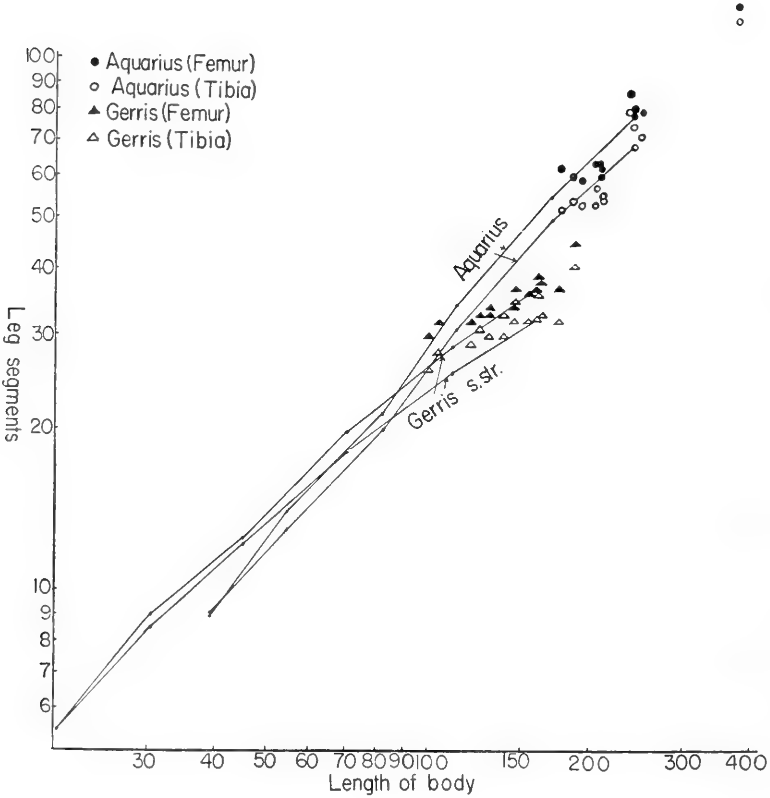
FIGURES 163, 164





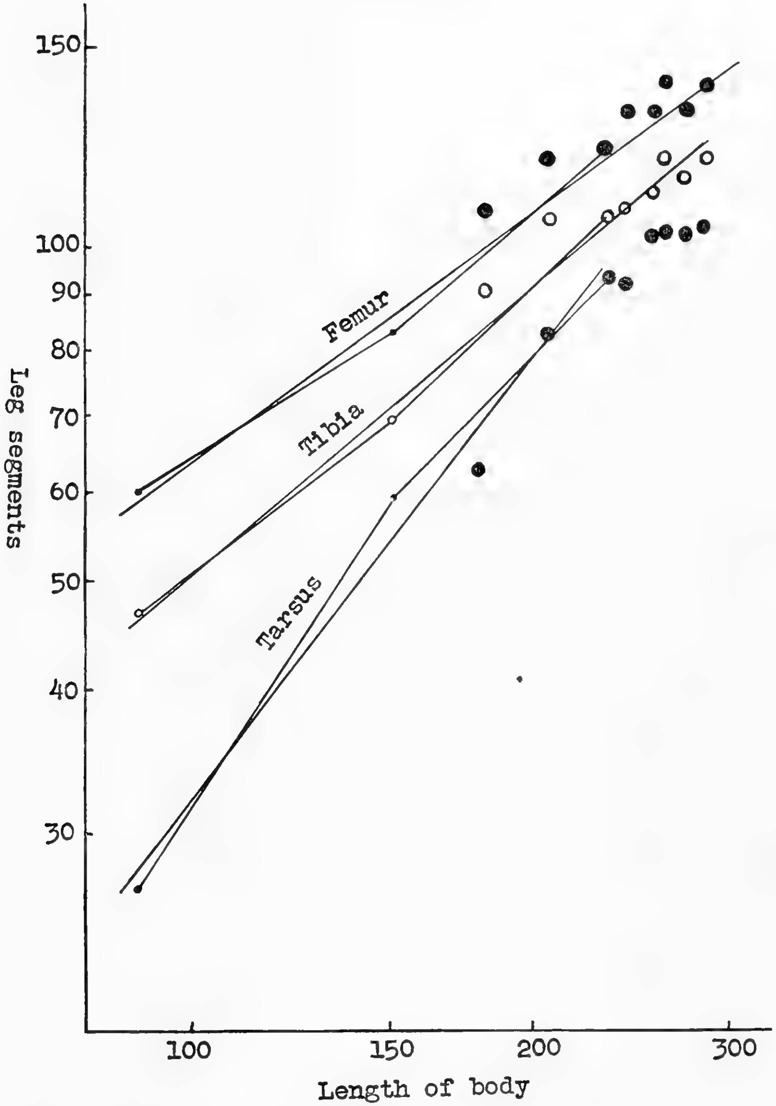
163. Middle leg segments in *Telmatometra* and related genera.
164. Middle leg segments in *Metrobates*.

FIGURE 165



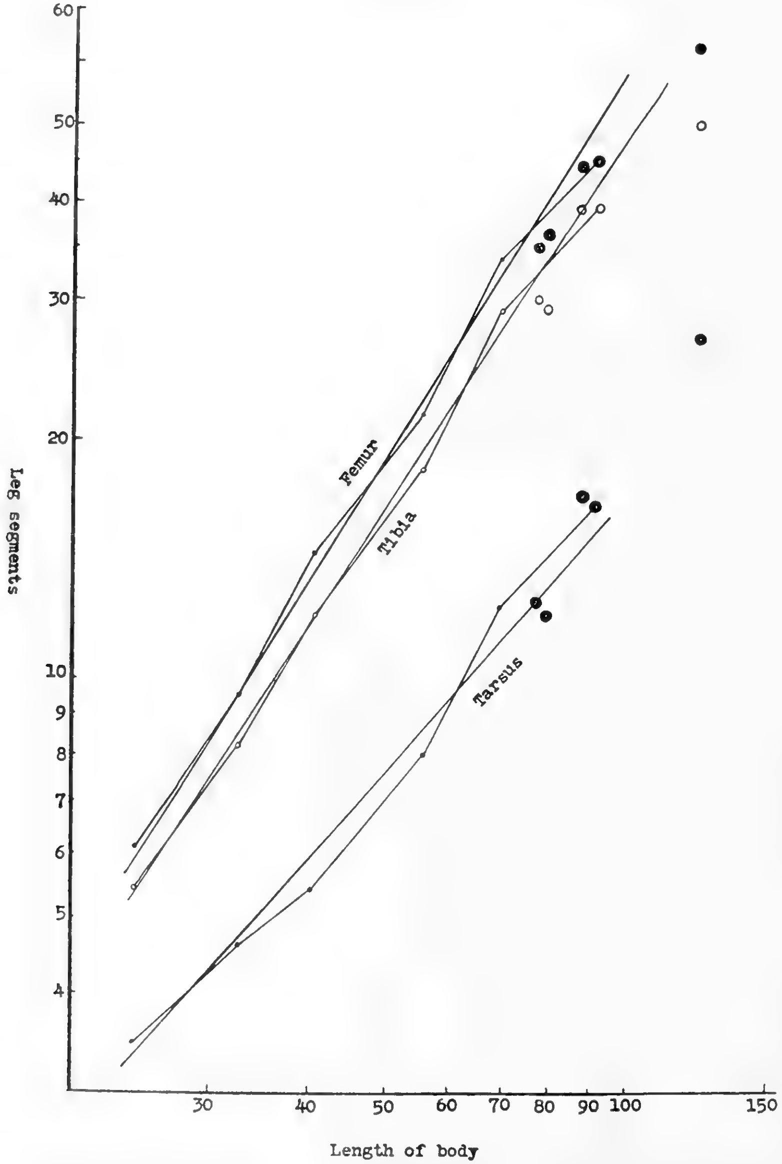
165. Front leg segments in *Gerris*. Round points for *Aquarius;* triangle points for *Gerris s. str.* Each connected point represents mean value at different stages.

Figure 166



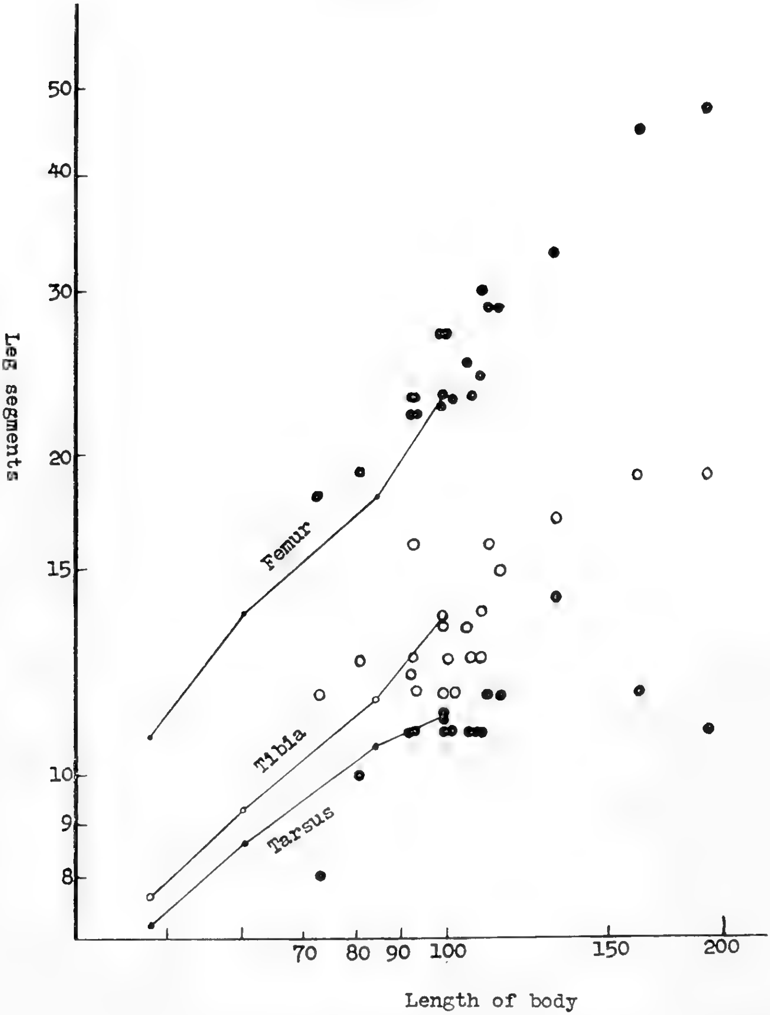
166. Front leg segments in *ptilomera.*

FIGURE 167



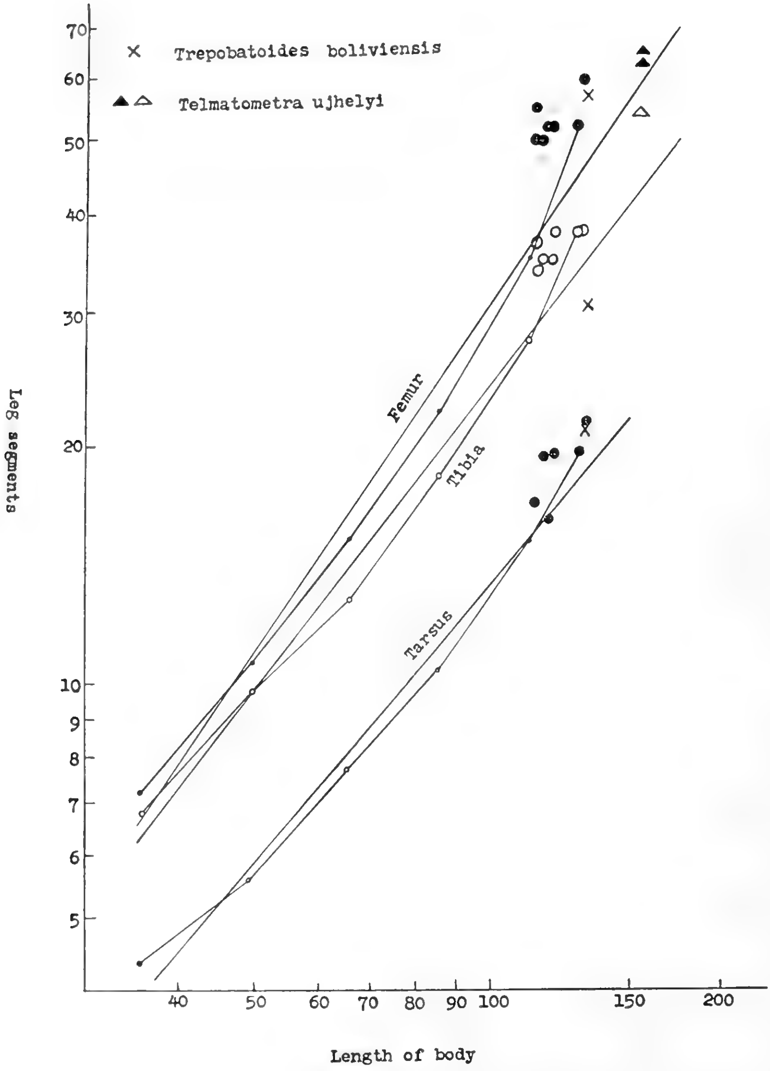
167. Front leg segments in *Metrocoris*. Each connected point represents mean value at different stages.

FIGURE 168



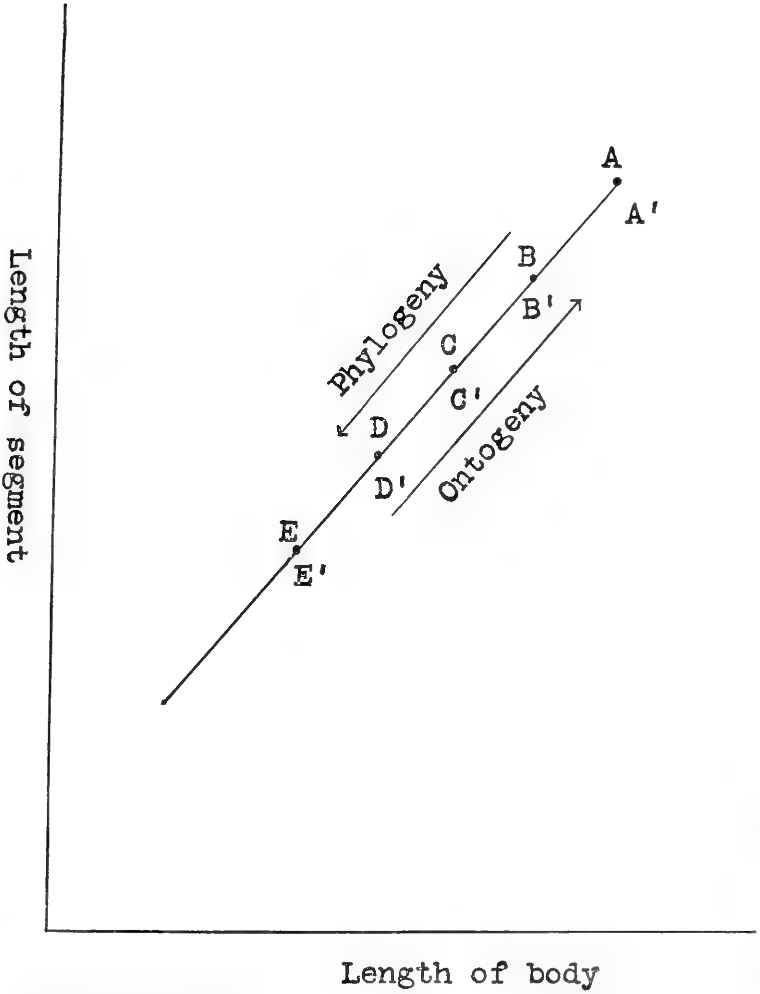
168. Front leg segments in Rhagadotarsinae. Each connected point represents mean value at different stages.

FIGURE 169



169. Front leg segments in *Trepobates* and related genera. Each connected point represents mean value at different stages.

FIGURE 170



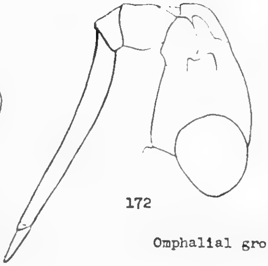
170. Diagram showing relation of ontogeny to phylogeny.

FIGURES 171-178

171. Dorsal view of body, *Gigantometra gigas* (China), winged male.
172. Lateral view of head, *Gigantometra gigas* (China).
173. Ventral view of metathorax, *Gigantometra gigas* (China).
174. Ventral view of male apical abdominal segments, *Gigantometra gigas* (China).
175. Lateral view of the male ninth and tenth abdominal segments, *Gigantometra gigas* (China).
176. Front tarsus, *Gigantometra gigas* (China).
177. Middle tarsus, *Gigantometra gigas* (China).
178. Hind tarsus, *Gigantometra gigas* (China).

Figures 171-178

171



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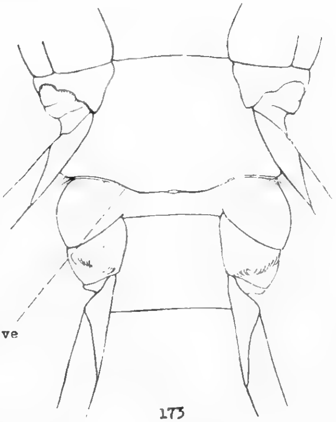

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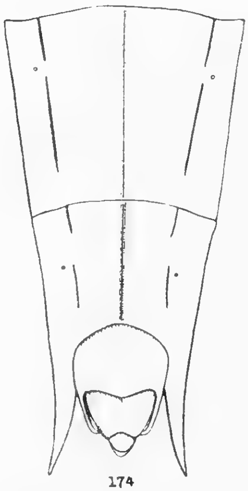

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FIGURES 179-192

179. Dorsal view of whole body, wingless male of *Gerris (Aquarius) cinereus* (Puton).

180. Ventral view of whole body, wingless male of *Gerris (Aquarius) cinereus* (Puton).

181. Lateral view of head, *Gerris (Aquarius) paludum* (Fabricius).

182. Antennae, *Gerris (Aquarius) paludum* (Fabricius).

183. Front leg, *Gerris (Aquarius) paludum* (Fabricius).

184. Middle tarsus, *Gerris (Aquarius) najas* (De Geer).

185. Hind tarsus, *Gerris (Aquarius) najas* (De Geer).

186. Female genitalia, *Gerris (Aquarius) elongatus* (Uhler).

187. Dorsal view of whole body, wingless female of *Gerris (Gerris) incognitus* Drake and Harris.

188. Lateral view of head, *Gerris (Gerris) thoracicus* Schummel.

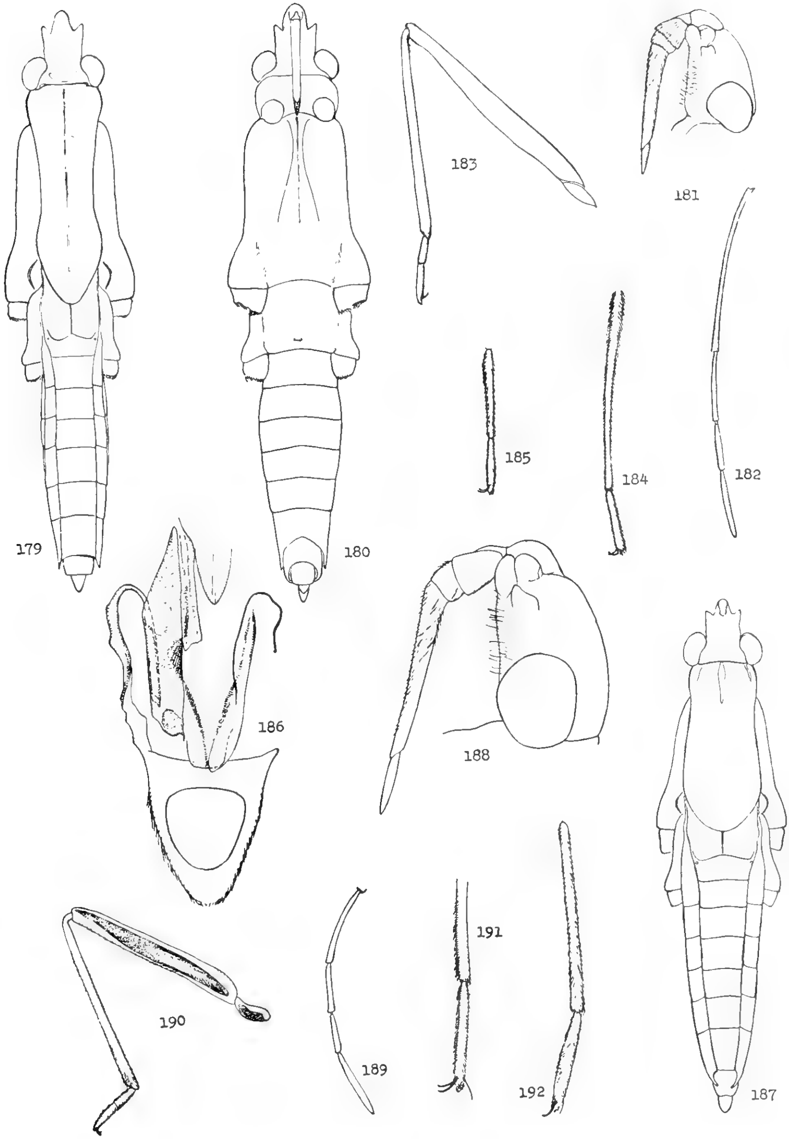
189. Antenna, *Gerris (Gerris) thoracicus* Schummel.

190. Front leg, *Gerris (Gerris) thoracicus* Schummel.

191. Middle tarsus, *Gerris (Gerris) costae* (Herrich-Schaeffer).

192. Hind tarsus, *Gerris (Gerris) costae* (Herrich-Schaeffer).

Figures 179-192



FIGURES 193-208

193. Ventral view of male apical abdominal segments, *Gerris (Aquarius) elongatus* (Uhler).

194. Same, *Gerris (Gerris) gibbifer* Schummel.

195. Same, *Gerris (Aquarius) remigis* Say.

196. Same, *Gerris (Aquarius) paludum* (Fabricius).

197. Same, *Gerris (Gerris) thoracicus* Schummel.

198. Same, *Gerris (Gerris) odontogaster* (Zetterstedt).

199. Same, *Gerris (Gerris) agrenticollis* Parshley.

200. Same, *Gerris (Gerris) firmus* Drake and Harris.

201. Same, *Gerris (Gerris) gillettei* Lethierry et Severin.

202. Same, *Gerris (Gerris) pingreensis* Drake and Harris.

203. Lateral view of abdomen, *Gerris (Gerris) firmus* Drake and Harris.

204. Ventral view of female apical abdominal segments, *Gerris (Aquarius) elongatus* (Uhler).

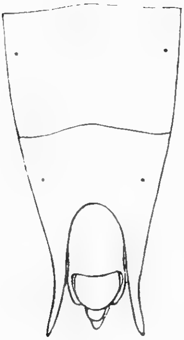
205. Same, *Gerris (Gerris) marginatus* Say.

206. Same, *Gerris (Aquarius) antigone* Kirkaldy.

207. Same, *Gerris (Gerris) odontogaster* (Zetterstedt).

208. Same, *Gerris (Aquarius) remigis* Say.

FIGURES 193-208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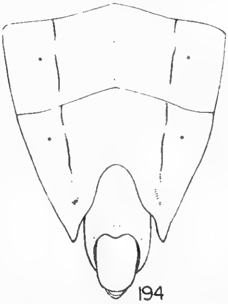
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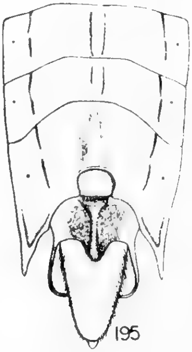
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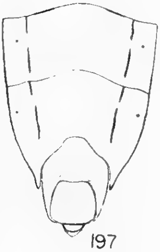
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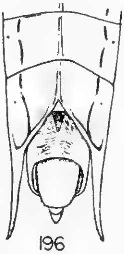
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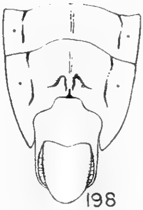
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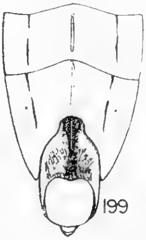
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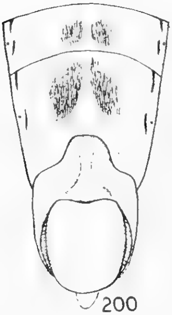
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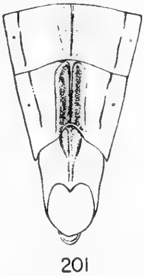
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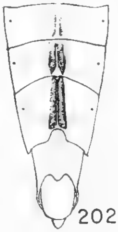
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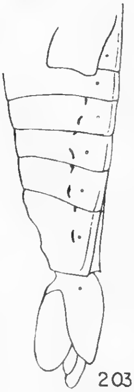
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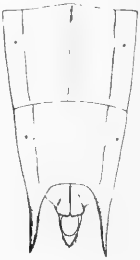
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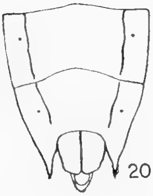
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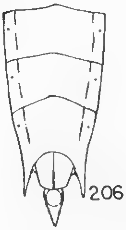
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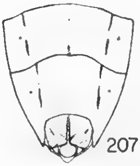
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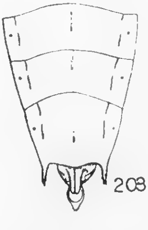
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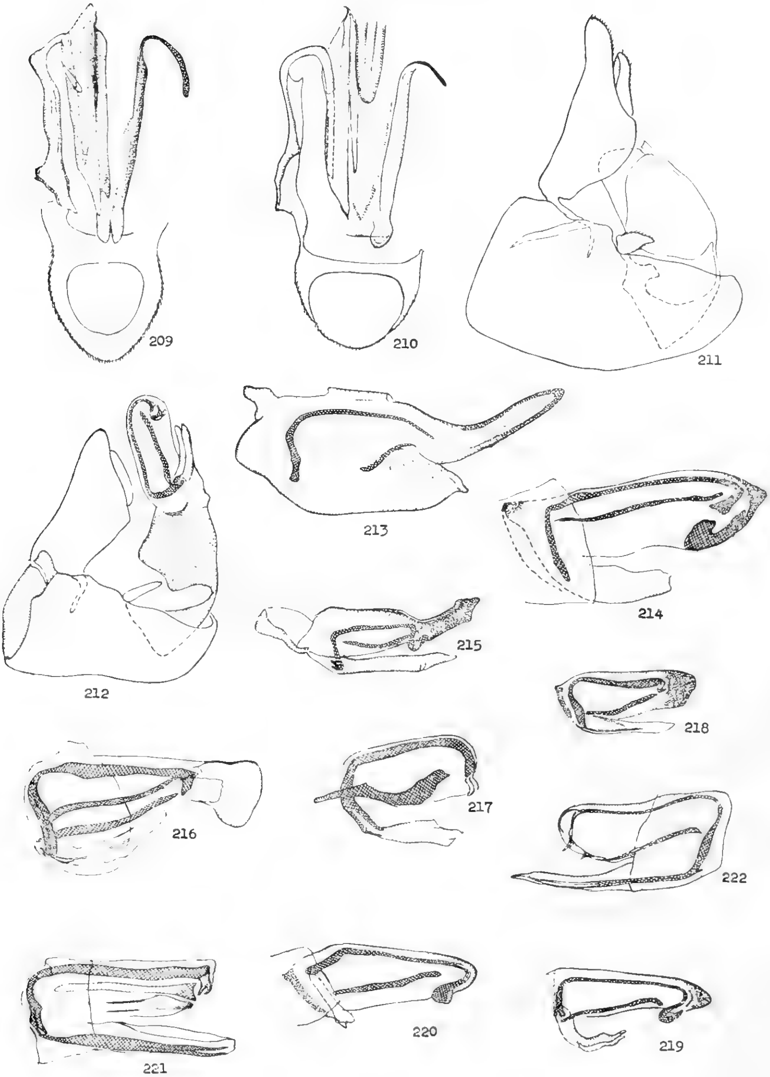
FIGURES 209-222

209. Female genitalia, *Gerris (Gerris) gillettei* Drake and Harris.
210. Female genitalia, *Gerris (Gerris) marginatus* Say.
211. Male genital segment, *Gerris (Aquarius) paludum* (Fabricius).
212. Male genital segment, *Gerris (Aquarius) elongatus* (Uhler).
213. Apical segment of endosoma, *Gerris (Aquarius) remigis* Say.
214. Same, *Gerris (Aquarius) chilensis* (Berg).
215. Same, *Gerris (Aquarius) amplus* Drake and Harris.
216. Same, *Gerris (Aquarius) paludum* (Fabricius).
217. Same, *Gerris (Aquarius) ventralis* (Fieber).
218. Same, *Gerris (Aquarius) antigone* Kirkaldy.
219. Same, *Gerris (Aquarius) conformis* (Uhler).
220. Same, *Gerris (Aquarius) cinereus* (Puton).
221. Same, *Gerris (Gerris) thoracicus* Schummel.
222. Same, *Gerris (Gerris) marginatus* Say.

FIGURES 209-222



FIGURES 223-233

223. Dorsal view of wingless female, *Gerris (Limnoporus) canaliculatus* Say.

224. Dorsal view of winged female, *Gerris (Limnoporus) rufoscutellatus* (Latreille).

225. Ventral view of winged female, *Gerris (Limnoporus) rufoscutellatus* (Latreille).

226. Dorsal view of the thorax in winged form, *Gerris (Limnoporus) dissortis* Drake and Harris.

227. Lateral view of the head, *Gerris (Limnoporus) rufoscutellatus* Latreille.

228. Antenna, *Gerris (Limnoporus) rufoscutellatus* Latreille.

229. Front leg, *Gerris (Limnoporus) rufoscutellatus* Latreille.

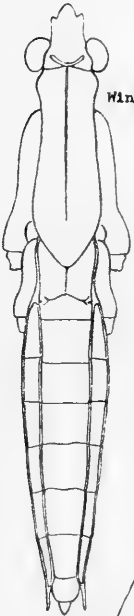
230. Hind wing, *Gerris (Limnoporus) dissortis* Drake and Harris.

231. Female genitalia, *Gerris (Limnoporus) notabilis* Drake and Hottes.

232. Apical segment of endosoma, *Gerris (Limnoporus) dissortis* Drake and Harris.

233. Same, *Gerris (Limnoporus) canaliculatus* Say.

FIGURES 223-233



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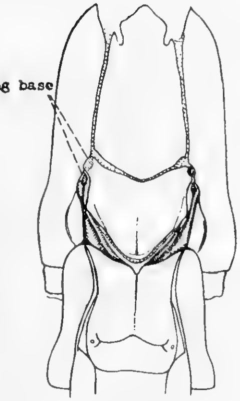

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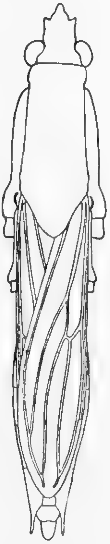

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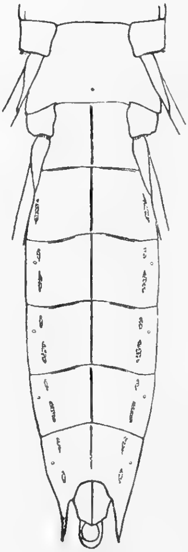

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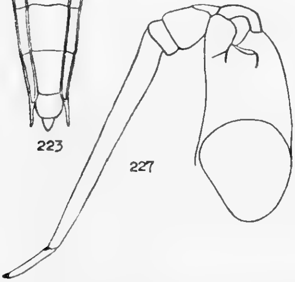

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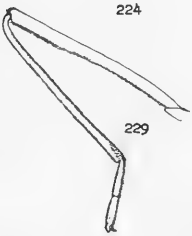

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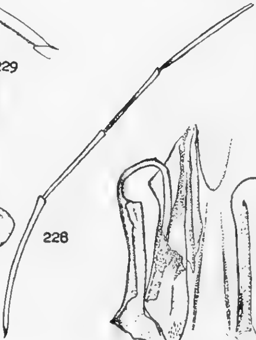

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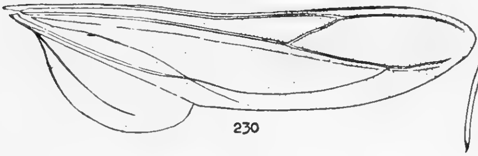

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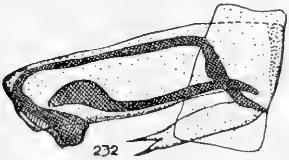

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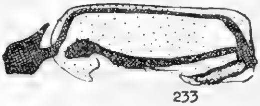

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FIGURES 234-242

234. Ventral view of wingless male, *Gerriselloides brachynotus* (Horváth).

235. Dorsal view of wingless male, *Gerriselloides brachynotus* (Horváth).

236. Lateral view of head, *Gerriselloides brachynotus* (Horváth).

237. Ventral view of male apical abdominal segments, *Gerriselloides brachynotus* (Horváth).

238. Lateral view of female apical abdominal segments, *Gerriselloides brachynotus* (Horváth).

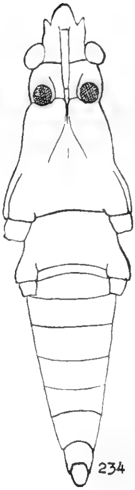
239. Male front leg, *Gerriselloides brachynotus* (Horváth).

240. Male antenna, *Gerriselloides brachynotus* (Horváth).

241. Middle leg, *Gerriselloides brachynotus* (Horváth).

242. Hind leg, *Gerriselloides brachynotus* (Horváth).

Figures 234-242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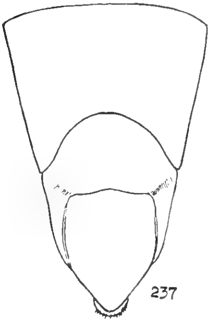
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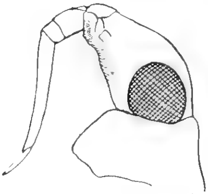
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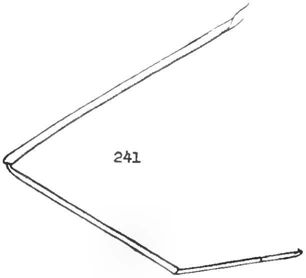
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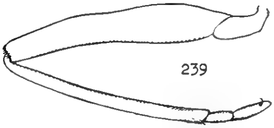
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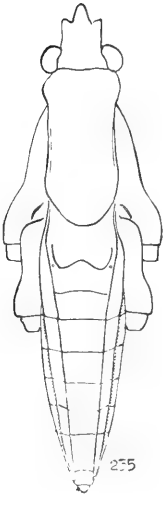
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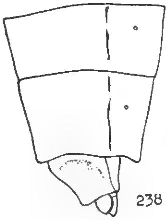
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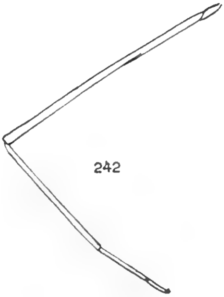
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FIGURES 243-251

243. Dorsal view of winged male, *Gerrisella settembrinoi* (Poisson).

244. Dorsal view of wingless male, *Gerrisella settembrinoi* (Poisson).

245. Lateral view of female head, *Gerrisella settembrinoi* (Poisson).

246. Ventral view of female abdomen, *Gerrisella settembrinoi* (Poisson).

247. Lateral view of male apical abdominal segments, *Gerrisella settembrinoi* (Poisson).

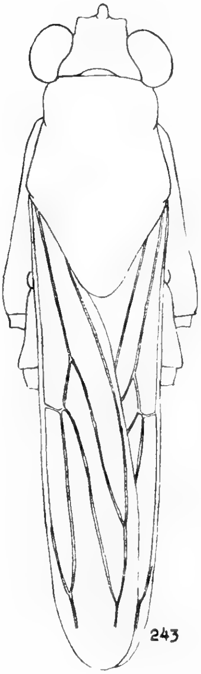
248. Female antenna, *Gerrisella settembrinoi* (Poisson).

249. Male front leg, *Gerrisella settembrinoi* (Poisson).

250. Male middle tarsus, *Gerrisella settembrinoi* (Poisson).

251. Male hind tibia and tarsus, *Gerrisella settembrinoi* (Poisson).

FIGURES 243-251



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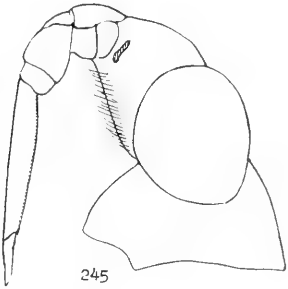

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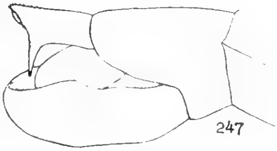

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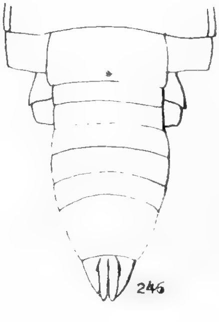

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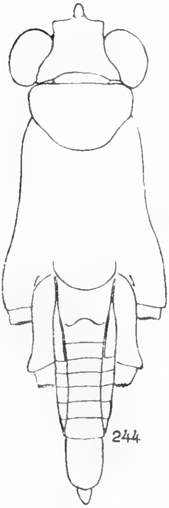

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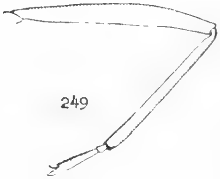

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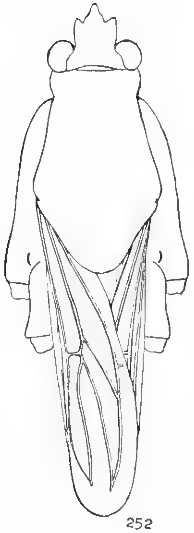
FIGURES 252-262

252. Dorsal view of winged female, *Tenagogerris euphrosyne* (Kirkaldy).
253. Pronotum in winged female, *Tenogogerris euphrosyne* (Kirkaldy).
254. Dorsal view of wingless female, *Tenagogerris euphrosyne* (Kirkaldy).
255. Ventral view of male abdomen, *Tenagogerris euphrosyne* (Kirkaldy).
256. Ventral view of female apical abdominal segments, *Tenagogerris euphrosyne* (Kirkaldy).
257. Lateral view of male genital segment, *Tenagogerris euphyrosyne* (Kirkaldy).
258. Male antenna, *Tenagogerris euphrosyne* (Kirkaldy).
259. Female genitalia, *Tenagogerris euphrosyne* (Kirkaldy).
260. Male front leg, *Tenagogerris euphrosyne* (Kirkaldy).
261. Male middle tarsus, *Tenagogerris euphrosyne* (Kirkaldy).
262. Male hind tarsus, *Tenagogerris euphrosyne* (Kirkaldy).

FIGURES 252-262



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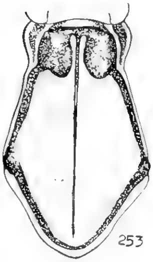

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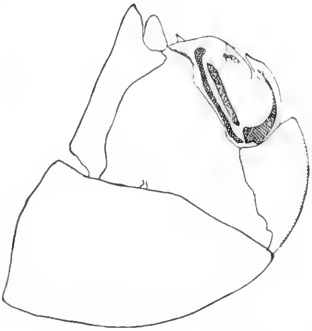

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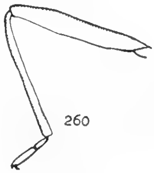

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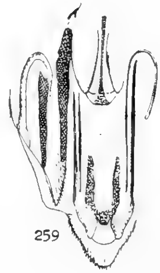

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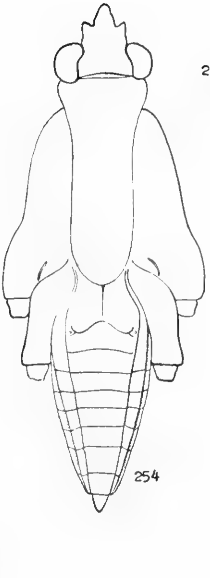

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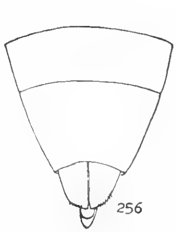

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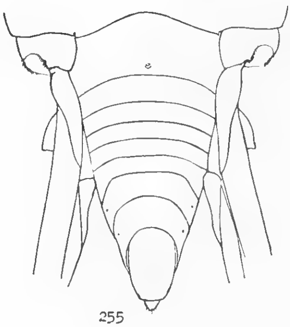

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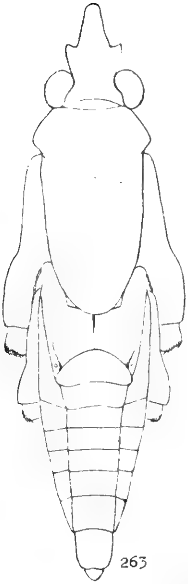
FIGURES 263-273

263. Dorsal view of wingless male, *Eurygerris mexicanus* (Champion).
264. Dorsal view of wingless male, *Eurygerris fuscinervis* (Berg).
265. Dorsal view of wingless female, *Eurygerris flavolineatus* (Champion).
266. Forewing, *Eurygerris cariniventris,* (Champion).
267. Lateral view of head, *Eurygerris fuscinervis* (Berg).
268. Pronotum in winged form, *Eurygerris fuscinervis* (Berg).
269. Front leg, *Eurygerris fuscinervis* (Berg).
270. Lateral view of male genital segment, *Eurygerris fuscinervis* (Berg).
271. Apical segment of endosoma, *Eurygerris mexicanus* (Champion).
272. Apical segment of endosoma, *Eurygerris fuscinervis* (Berg).
273. Antenna, *Eurygerris fuscinervis* (Berg).

Figures 263-273



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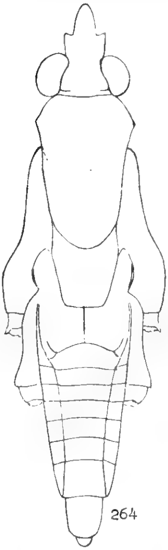

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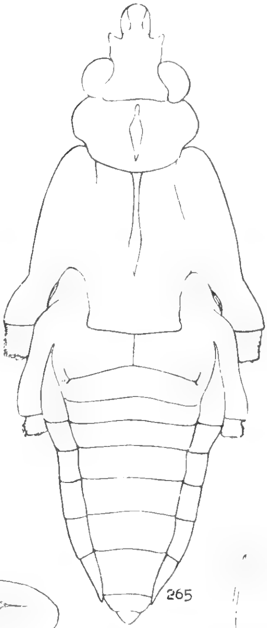

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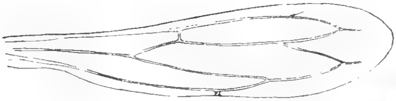

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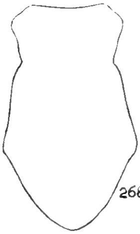

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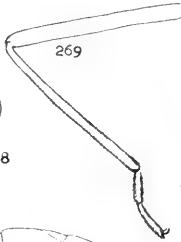

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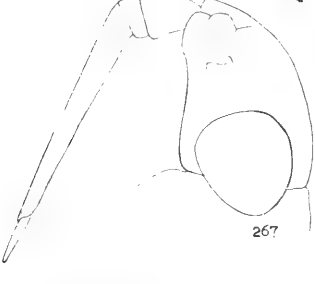

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FIGURES 274-287

274. Ventral view of male abdomen, *Eurygerris fuscinervis* (Berg).

275. Ventral view of male apical abdominal segments, *Eurygerris mexicanus* (Champion).

276. Ventral view of male apical abdominal segments, *Eurygerris carmelus* (Drake and Harris).

277. Ventral view of male apical abdominal segments, *Eurygerris flavolineatus* (Champion).

278. Apical segment of endosoma, *Eurygerris carmelus,* (Drake and Harris).

279. Lateral view of female apical abdominal segments, *Eurygerris mexicanus* (Champion).

280. Lateral view of female apical abdominal segments, *Eurygerris carmelus* (Drake and Harris).

281. Female genitalia, *Eurygerris mexicanus* (Champion).

282. Male front femur, *Eurygerris flavolineatus* (Champion).

283. Same, *Eurygerris mexicanus* (Champion).

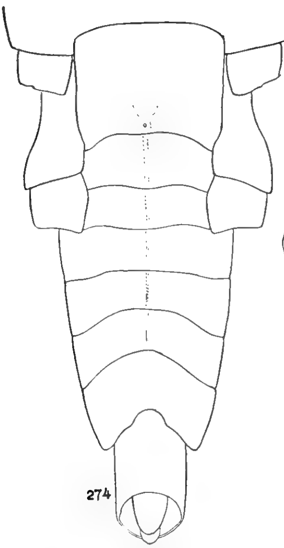
284. Same, *Eurygerris cariniventris* (Champion).

285. Same, *Eurygerris carmelus* (Drake and Harris).

286. Same, *Eurygerris kahli* (Drake and Harris).

287. Same, *Eurygerris fuscinervis* (Berg).

FIGURES 274-287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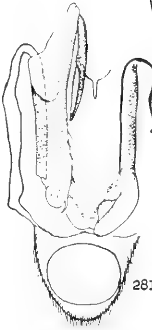
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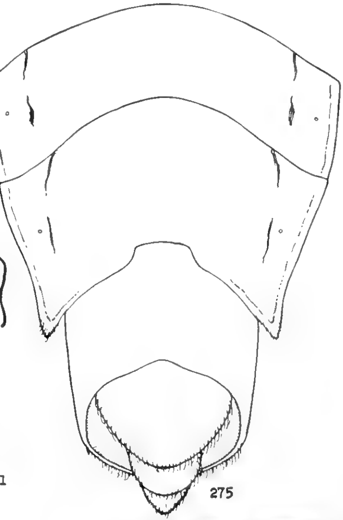
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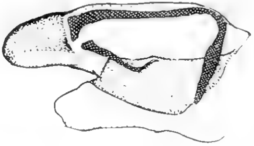
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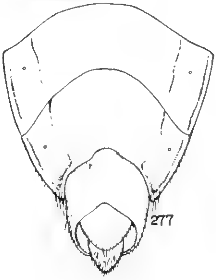
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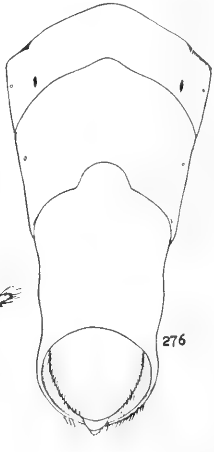
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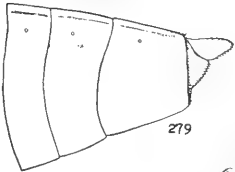
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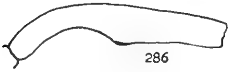
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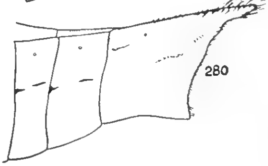
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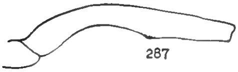
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FIGURES 288-301

288. Dorsal view of wingless female, ***Limnogonus (Limnogonus) hypoleucus*** (Gerstaecker).

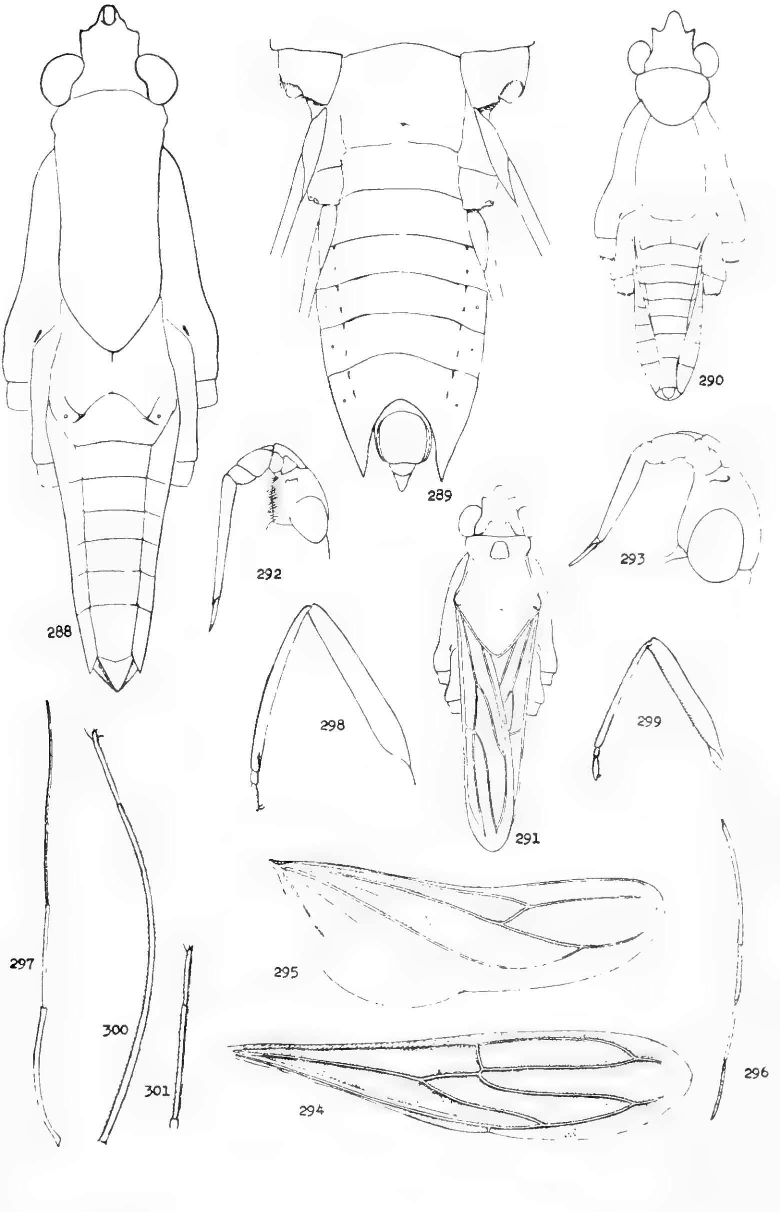
289. Ventral view of male abdomen, ***Limnogonus (Limnogonus) hypoleucus*** (Gerstaecker).

290. Dorsal view of wingless female, ***Limnogonus (Limnogonellus) hesione*** (Kirkaldy).

291. Dorsal view of winged male, ***Limnogonus (Limnogonellus) lubricus*** B.-White.

292. Lateral view of head, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
293. Lateral view of head, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).
294. Forewing, *Limnogonus (Limnogonellus) lubricus* B.-White.
295. Hind wing, *Limnogonus (Limnogonellus) lubricus* B.-White.
296. Antenna, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).
297. Antenna, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
298. Front leg, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
299. Front leg, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).
300. Middle tarsus, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
301. Middle tarsus, *Limnogonus (Limnogonus) hyalinus* (Fabricius).

FIGURES 288-301



FIGURES 302-320

302. Ventral view of male abdomen, *Limnogonus (Limnogonus) guerini* (Lethierry et Severin).

303. Ventral view of apical abdominal segments, *Limnogonus (Limnogonus) nitidus* (Mayr).

304. Same, *Limnogonus (Limnogonus) aduncus* Drake and Harris.

305. Same, *Limnogonus (Limnogonus) aduncus* Drake and Harris.

306. Same, *Limnogonus (Limnogonus) hyalinus* (Fabricius).

307. Lateral view of apical abdominal segments, *Limnogonus (Limnogonus) recurvus* Drake and Harris.

308. Same, *Limnogonus (Limnogonus) lundbladi* Usinger.

309. Dorsal view of male apical abdominal segments, *Limnogonus (Limnogonellus) visendus* Drake and Harris.

310. Ventral view of female apical abdominal segments, *Limnogonus (Limnogonus) hypoleucus* (Gerstaecker).

311. Ventral view of female apical abdominal segments, *Limnogonus (Limnogonus) guerini* (Lethierry et Severin).

312. Lateral view of female apical abdominal segments, *Limnogonus nitidus* (Mayr).

313. Same, *Limnogonus (Limnogonus) ignotus* Drake and Harris.

314. Ventral view of female apical abdominal segments, *Limnogonus (Limnogonus) hyalinus* (Fabricius).

315. Lateral view of female apical abdominal segments, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).

316. Ventral view of female apical abdominal segments, *Limnogonus (Limnogonus) lundbladi* Usinger.

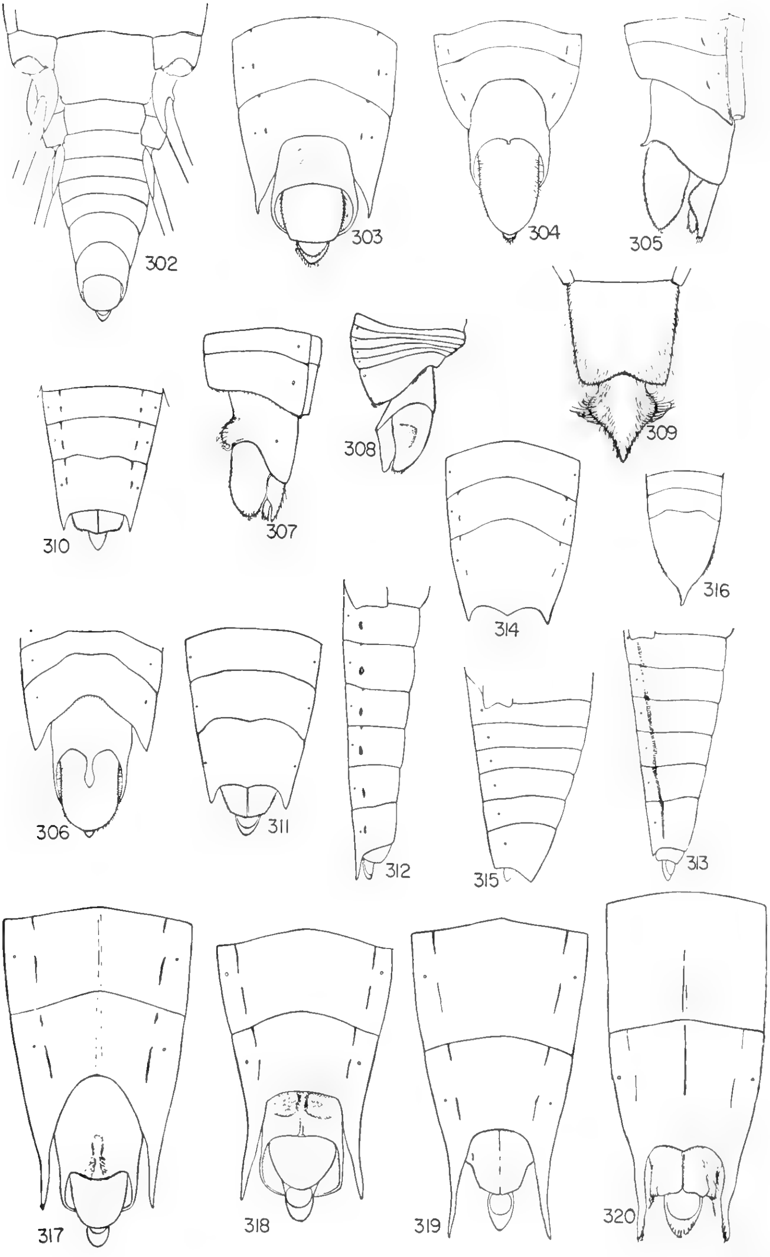
317. Ventral view of male apical abdominal segments, *Gerris (Limnoporus) rufoscutellatus* Latreille.

318. Same, *Gerris (Limnoporus) canaliculatus* Say.

319. Ventral view of female apical abdominal segments, *Gerris (Limnoporus) notabilis* Drake and Hottes.

320. Same, *Gerris (Limnoporus) canaliculatus* Say.

Figures 302-320



FIGURES 321-334

321. Lateral view of male genital segment, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).

322. Lateral view of male genital segment, *Limnogonus (Limnogonus) hyalinus* (Fabricius).

323. Female genitalia, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).

324. Female genitalia, *Limnogonus (Limnogonus) hyalinus* (Fabricius).

325. Apical segment of endosoma, *Limnogonus (Limnogonus) aduncus* Drake and Harris.

326. Same, *Limnogonus (Limnogonus) cereiventris leptocerus* (Reuter).

327. Same, *Limnogonus (Limnogonus) hyalinus* (Fabricius).

328. Same, *Limnogonus (Limnogonus) australis* (Skuse).

329. Same, *Limnogonus (Limnogonus) fossarum* (Fabricius).

330. Same, *Limnogonus (Limnogonus) hypoleucus* (Gerstaecker).

331. Same, *Limnogonus (Limnogonus) nitidus* (Mayr).

332. Same, *Limnogonus (Limnogonellus) lubricus* White.

333. Same, *Limnogonus (Limnogonellus) visendus* Drake and Harris.

334. Same, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).

Figures 321-334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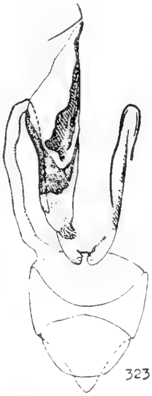
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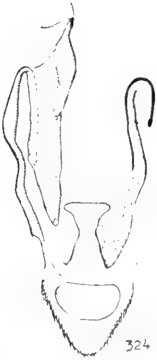
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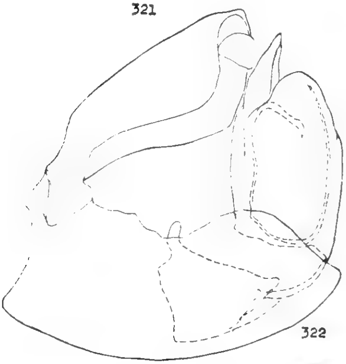
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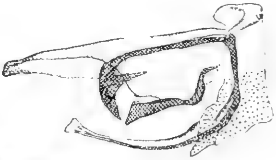
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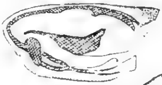
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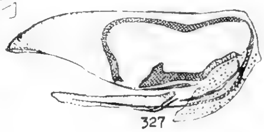
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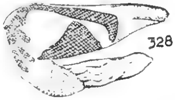
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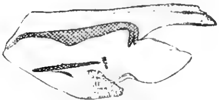
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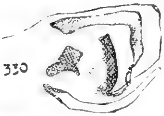
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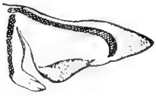
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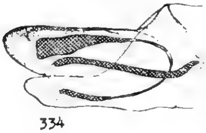
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FIGURES 335-345

335. Dorsal view of winged male, *Tachygerris adamsoni* (Drake).

336. Ventral view of male abdomen, *Trachygerris celocis* (Drake and Harris).

337. Dorsal view of structures beneath wings, *Tachygerris celocis* (Drake and Harris).

338. Lateral view of thorax, *Tachygerris adamsoni* (Drake).

339. Lateral view of head, *Tachygerris adamsoni* (Drake).

340. Hind wing, *Tachygerris celocis* (Drake and Harris).

341. Antenna, *Tachygerris adamsoni* (Drake).

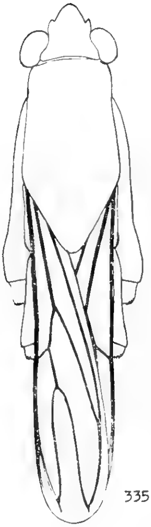
342. Lateral view of male genital segment, *Tachygerris celocis* (Drake and Harris).

343. Female front leg, *Tachygerris adamsoni* (Drake).

344. Middle tarsus, *Tachygerris spinulatus* (Kuitert).

345. Hind tarsus, *Tachygerris spinulatus* (Kuitert).

Figures 335-345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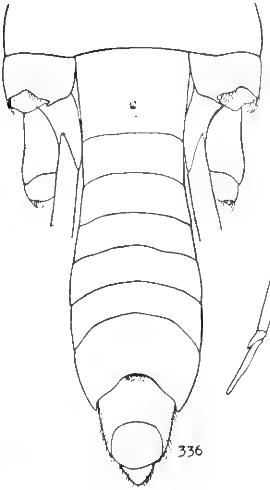
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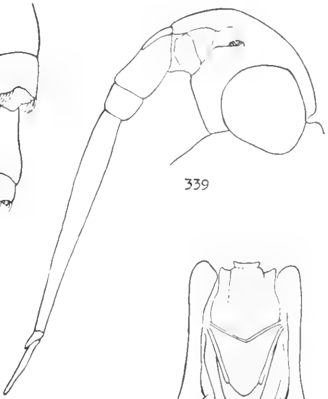
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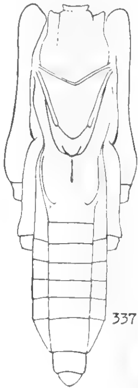
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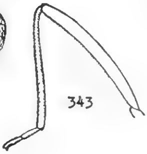
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FIGURES 346-358

346. Ventral view of female apical abdominal segments, *Tachygerris quadrilineatus* (Champion).

347. Same, *Tachygerris celocis* (Drake and Harris).

348. Same, *Tachygerris spinulatus* (Kuitert).

349. Same, *Tachygerris adamsoni* (Drake).

350. Same, *Tachygerris opacus* (Champion).

351. Same, *Tachygerris surinamensis* Hungerford and Matsuda.

352. Female genitalia, *Tachygerris opacus* (Champion).

353. Ventral view of apical abdominal segments, *Tachygerris celocis* (Drake and Harris).

354. Apical segment of endosoma, *Tachygerris spinulatus* (Kuitert).

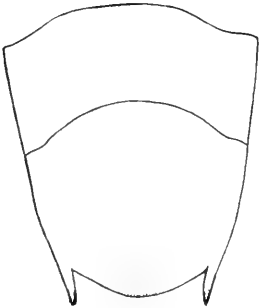
355. Same, *Tachygerris celocis* (Drake and Harris).

356. Same, *Tachygerris qudrilineatus* (Champion).

357. Male front leg, *Tachygerris celocis* (Drake and Harris).

358. Male front tarsus, *Tachygerris celocis* (Drake and Harris).

FIGURES 346-358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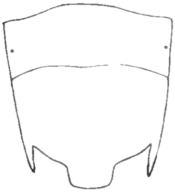
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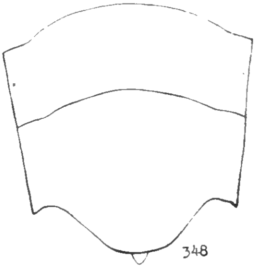
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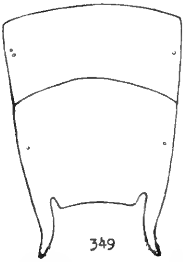
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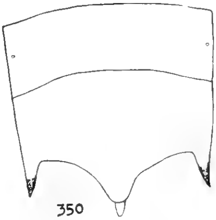
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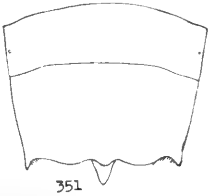
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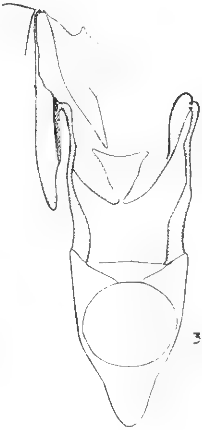
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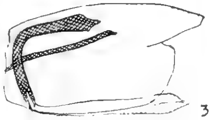
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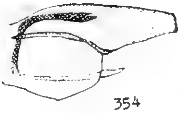
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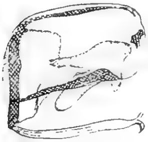
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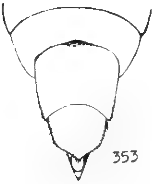
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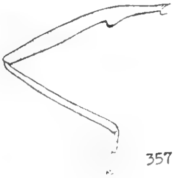
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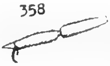
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FIGURES 359-368

359. Dorsal view of wingless female, *Tenagogonus (Limnometra) ciliatus* (Mayr).

360. Lateral view of head, *Tenagogonus (Limnometra) ciliatus* (Mayr).

361. Lateral view of male genital segment, *Tenagogonus (Limnometra) ciliatus* (Mayr).

362. Female genitalia, *Tenagogonus (Limnometra) ciliatus* (Mayr).

363. Forewing, *Tenagogonus (Limnometra) ciliatus* (Mayr).

364. Hind wing, *Tenagogonus (Limnometra) cursitans* (Fabricius).

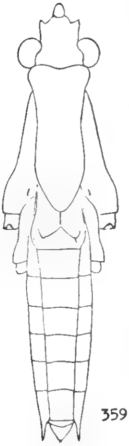
365. Ventral view of metathorax, *Tenagogonus (Limnometra) ciliatus* (Mayr).

366. Male front leg, *Tenagogonus (Limnometra) ciliatus* (Mayr).

367. Middle tarsus, *Tenagogonus (Limnometra) annulicornis* (Breddin).

368. Hind tarsus, *Tenogogonus (Limnometra) annulicornis* (Breddin).

Figures 359-368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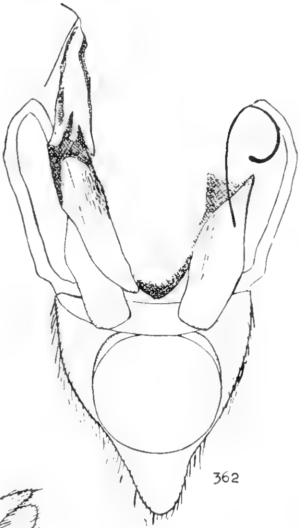
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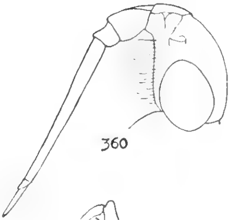
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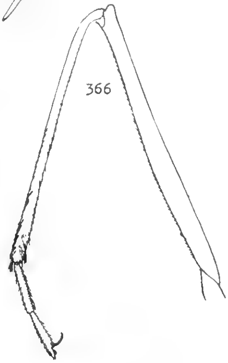
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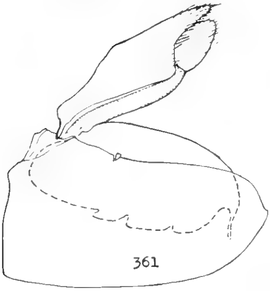
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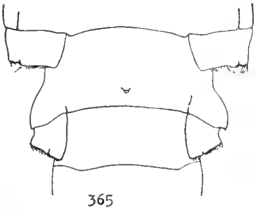
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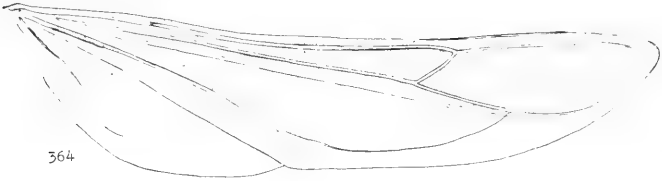
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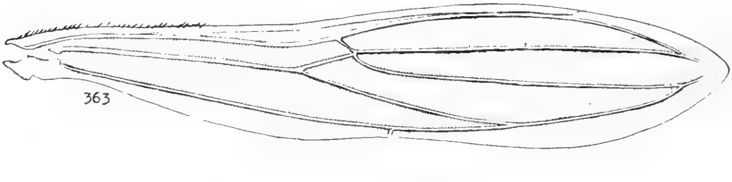
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FIGURES 369-377

369. Dorsal view of wingless female, *Tenagogonus (Tenagogonus) madagascariensis* Hoberlandt.

370. Dorsal view of wingless male, *Tenagogonus (Tenagogonus) albovittatus* (Stål).

371. Dorsal view of wingless male, *Tenagogonus (Tenagogonus) madagascariensis* Hoberlandt.

372. Lateral view of head, *Tenagogonus (Tenagogonus) albovittatus* Stål.

373. Lateral view of thorax in winged female, *Tenagogonus (Tenagogonus) fijiensis* Hungerford and Matsuda.

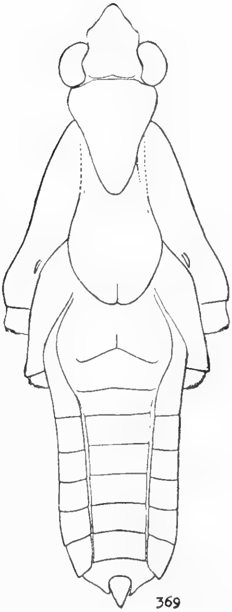
374. Ventral view of thorax and abdomen, *Tenagogonus (Tenagogonus) albovittatus* Stål.

375. Forewing, *Tenagogonus (Tenagogonus) pravipes bergrothi* Hungerford and Matsuda.

376. Hind wing, *Tenagogonus (Tenagogonus) pravipes bergrothi* Hungerford and Matsuda.

377. Male front leg, *Tenagogonus (Tenagogonus) albovittatus* Stål.

FIGURES 369-377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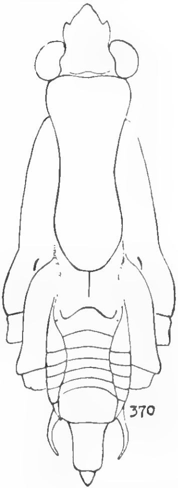
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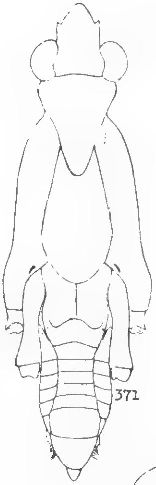
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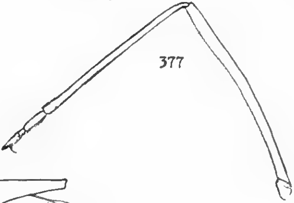
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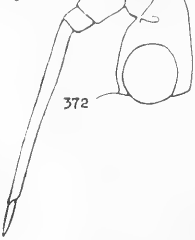
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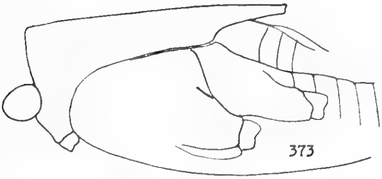
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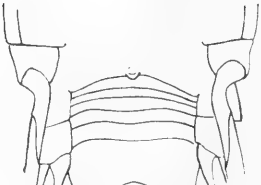
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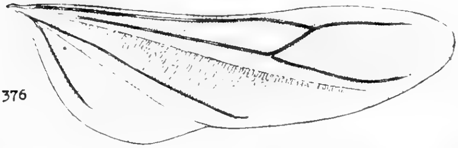
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FIGURES 378-387

378. Lateral view of male genital segment, *Tenagogonus (Tenagogonus) albovittatus* Stål.

379. Lateral view of male genital segment, *Tenagogonus (Tenagogonus) madagascariensis* Hoberlandt.

380. Apical segment of endosoma, *Tenagogonus (Limnometra) ciliatus* (Mayr).

381. Same, *Tenagogonus (Tenagogonus) madagascariensis* Hoberlandt.

382. Same, *Tenagogonus (Tenagogonus) albovittatus* Stål.

383. Same, *Tenagogonus (Limnometra) femoratus* (Mayr).

384. Female genitalia, *Tenagogonus (Limnometra) femoratus* (Mayr).

385. Same, *Tenagogonus (Tenagogonus) pravipes bergrothi* Hungerford and Matsuda.

386. Same, *Tenagogonus (Tenagogonus) madagascariensis* Hoberlandt.

387. Same, *Tenagogonus (Tenagogonus) albovittatus* Stål.

FIGURES 378-387


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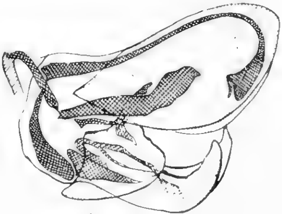
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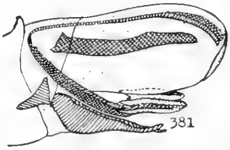
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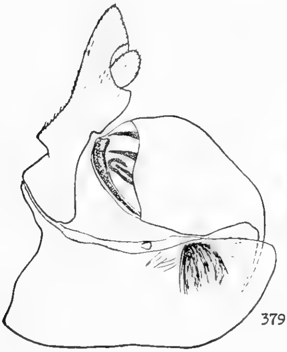
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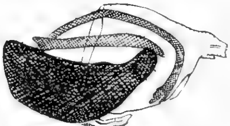
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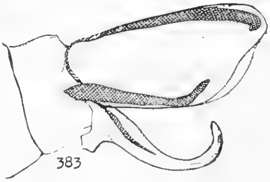
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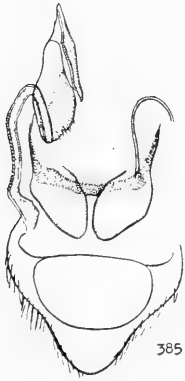
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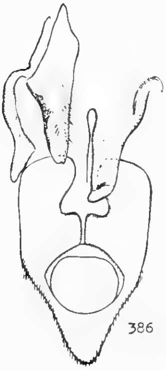
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FIGURES 388-406

388. Lateral view of male apical abdominal segment, *Tenagogonus (Limnometra) insularis* (Hungerford and Matsuda).

389. Same, *Tenagogonus (Limnometra) anadyomene* (Kirkaldy).

390. Same, *Tenagogonus (Tenagogonus) kuiterti* Hungerford and Matsuda.

391. Same, *Tenagogonus (Tenagogonus) zambezinus* (Poisson).

392. Same, *Tenagogonus (Tenagogonus) divergens* Hungerford and Matsuda.

393. Same, *Tenagogonus (Tenagogonus) madagascariensis* Hoberlandt.

394. Same, *Tenagogonus (Tenagogonus) albovittatus* Stål.

395. Same, *Tenagogonus (Tenagogonus) kampaspe* Kirkaldy.

396. Ventral view of male apical abdominal segments, *Tenagogonus (Limnometra) fluviorum* (Fabricius).

397. Same, *Tenagogonus (Limnometra) octopunctatus* (Hungerford).

398. Same, *Tenagogonus (Limnometra) lipovskii* (Hungerford and Matsuda).

399. Same, *Tenagogonus (Tenagogonus) kuiterti* Hungerford and Matsuda.

400. Same, *Tenagogonus (Tenagogonus) albovittatus* Stål.

401. Same, *Tenagogonus (Tenagogonus) madagascariensis* Hoberlandt.

402. Same, *Tenagogonus (Tenagogonus) robustus* Hungerford and Matsuda.

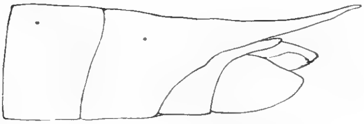
403. Ventral view of female apical abdominal segments, *Tenagogonus (Limnometra) ciliatus* (Mayr).

404. Same, *Tenagogonus (Limnometra) octopunctatus* (Hungerford).

405. Same, *Tenagogonus (Tenagogonus) pravipes bergrothi* Hungerford and Matsuda.

406. Same, *Tenagogonus (Tenagogonus) fijiensis* Hungerford and Matsuda.

FIGURES 388-406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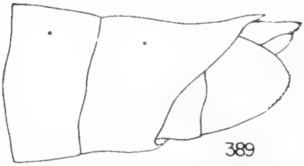
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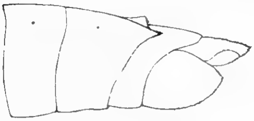
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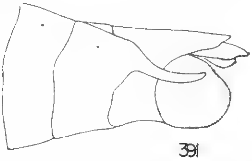
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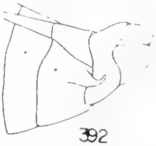
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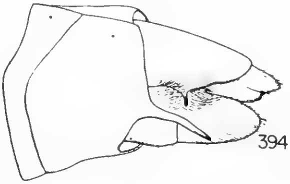
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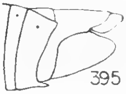
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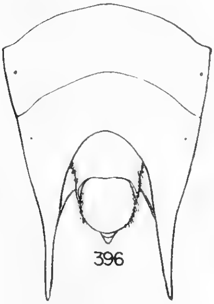
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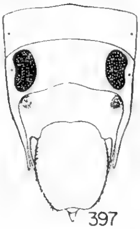
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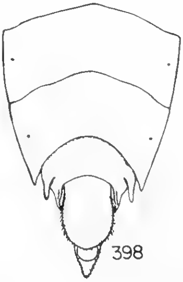
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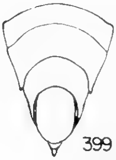
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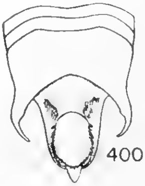
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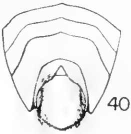
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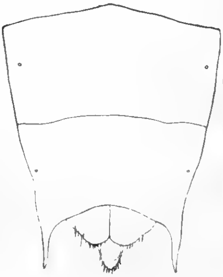
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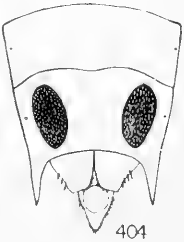
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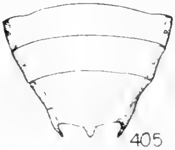
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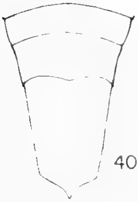
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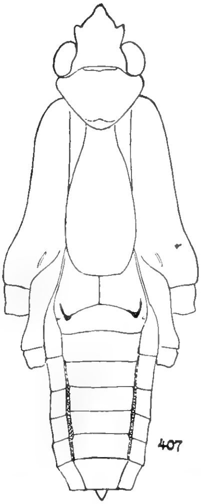
FIGURES 407-420

407. Dorsal view of wingless female, *Tenagogonus (Tenagometra)* sp.
408. Dorsal view of wingless male, *Tenagogonus (Tenagometra)* sp.
409. Lateral view of head, *Tenagogonus (Tenagometra)* sp.
410. Ventral view of male apical abdominal segments, *Tenagogonus (Tenagometra)* sp.
411. Ventral view of female abdomen, *Tenagogonus (Tenagogonus)* sp.
412. Lateral view of male genital segment, *Tenagogonus (Tenagometra)* sp.
413. Apical segment of endosoma, *Tenagogonus (Tenagometra)* sp.
414. Ventral view of female apical abdominal segments, *Tenagogonus (Tenagometra)* sp.
415. Female front leg *Tenagogonus (Tenagometra)* sp.
416. Dorsal view, *Tenagometrella grandiusculus* (Poisson).
417. Lateral view of head, *Tenagometrella grandiusculus* (Poisson).
418. Ventral view of abdomen, *Tenagometrella grandiusculus* (Poisson).
419. Lateral view of male genital segment, *Tenagometrella grandiusculus* (Poisson).
420. Male front leg, *Tenagometrella grandiusculus* (Poisson).

Figures 407-420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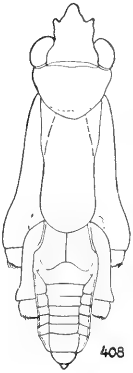
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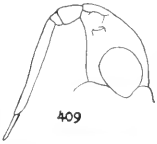
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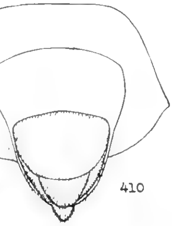
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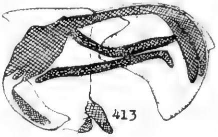
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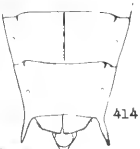
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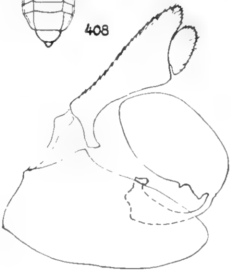
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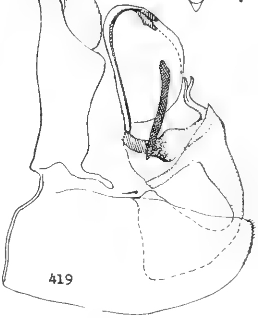
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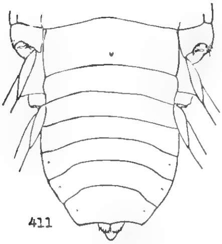
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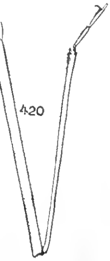
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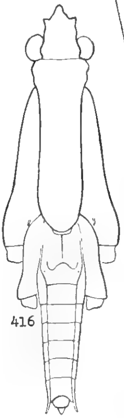
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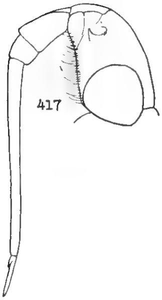
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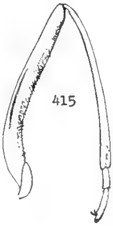
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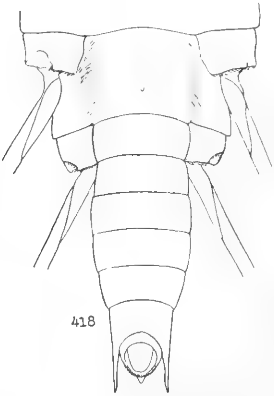
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FIGURES 421-432

421. Dorsal view of wingless male, *Cylindrostethus erythropus* (Herrich-Schaeffer).

422. Ventral view of metathorax and basal abdomen, *Cylindrostethus erythropus* (Herrich-Schaeffer).

423. Dorsal view of structures beneath wings, *Cylindrostethus productus* Spinola.

424. Lateral view of thorax, *Cylindrostethus productus* Spinola.

425. Dorsal view of female metathorax and basal abdomen, *Cylindrostethus bilobatus* Kuitert.

426. Ventral view of male mesothorax, *Cylindrostethus bilobatus* Kuitert.

427. Antenna, *Cylindrostethus erythropus* (Herrich-Schaeffer).

428. Forewing, *Cylindrostethus erythropus* (Herrich-Schaeffer).

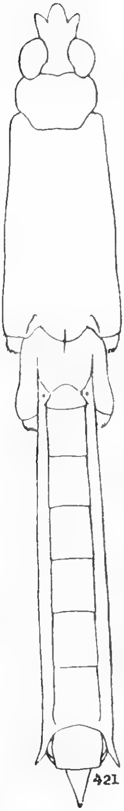
429. Hind wing, *Cylindrostethus erythropus* (Herrich-Schaeffer).

430. Front leg, *Cylindrostethus erythropus* (Herrich-Schaeffer).

431. Middle tarsus, *Cylindrostethus productus* Spinola.

432. Hind tarsus, *Cylindrostethus productus* Spinola.

Figures 421-432



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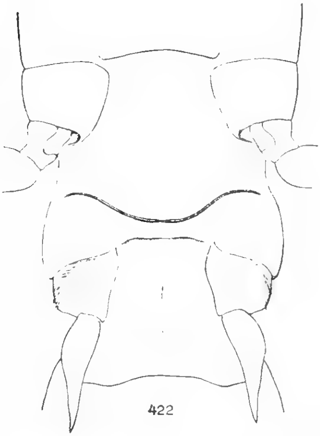

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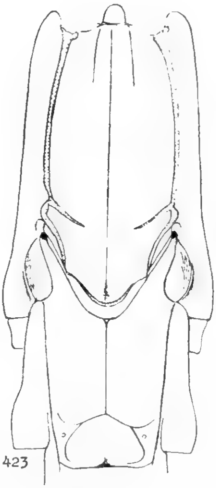

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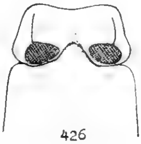

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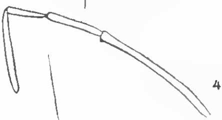

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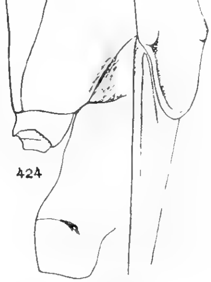

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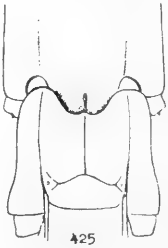

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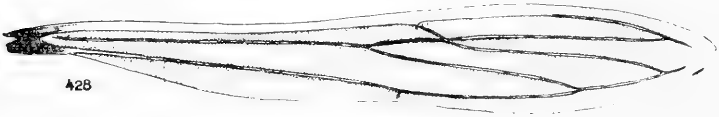

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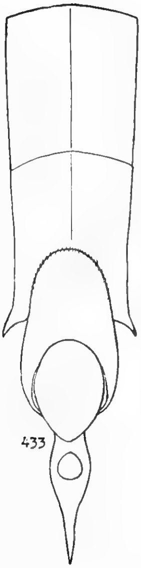
FIGURES 433-446

433. Ventral view of male apical abdominal segments, *Cylindrostethus regulus* (B.-White).
434. Same, *Cylindrostethus hungerfordi* Drake and Harris.
435. Same, *Cylindrostethus costalis* Schmidt.
436. Same, *Cylindrostethus palmaris* Drake and Harris.
437. Same, *Cylindrostethus bilobatus* Kuitert.
438. Same, *Cylindrostethus erythropus* (Herrich-Schaeffer).
439. Same, *Cylindrostethus bassleri* Drake.
440. Same, *Cylindrostethus linearis* (Erichson).
441. Same, *Cylindrostethus productus* Spinola.
442. Same, *Cylindrostethus naiades* Kirkaldy.
443. Same, *Cylindrostethus sumatranus* Lundblad.
444. Same, *Cylindrostethus vittipes* Stål.
445. Same, *Cylindrostethus persephone* Kirkaldy.
446. Same, *Cylindrostethus nietneri* Schmidt.

FIGURES 433-446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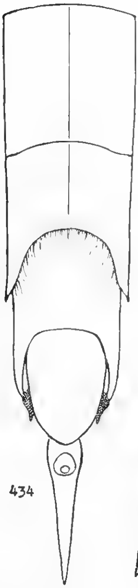
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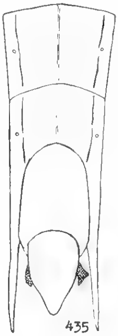
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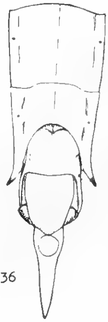
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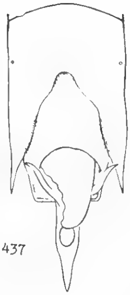
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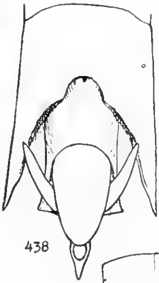
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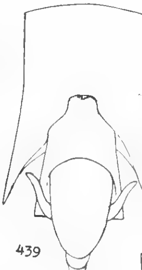
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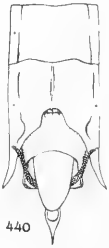
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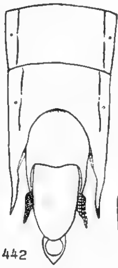
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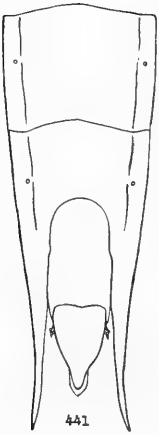
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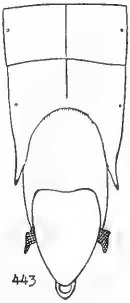
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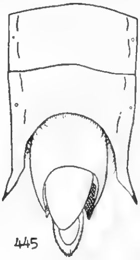
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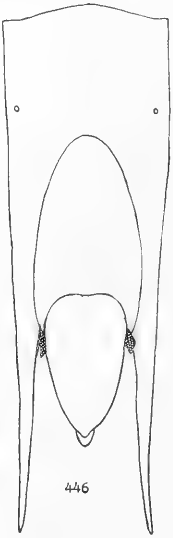
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FIGURES 447-459

447. Lateral view of female apical abdominal segments, *Cylindrostethus productus* Spinola.

448. Lateral view of female apical abdominal segments, *Cylindrostethus palmaris* Drake and Harris.

449. Ventral view of female apical abdominal segments, *Cylindrostethus palmaris,* Drake and Harris.

450. Lateral view of female apical abdominal segments, *Cylindrostethus linearis* (Erichson).

451. Same, *Cylindrostethus sumatranus* Lundblad.

452. Lateral view of head, *Cylindrostethus erythropus* (Herrich-Schaeffer).

453. Female genitalia, *Cylindrostethus productus* Spinola.

454. Female genitalia, *Cylindrostethus erythropus* (Herrich-Schaeffer).

455. Lateral view of male genital segment, *Cylindrostethus erythropus* (Herrich-Schaeffer).

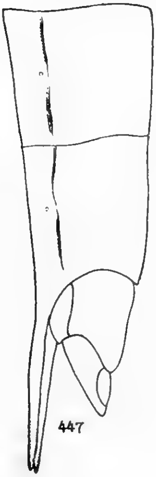
456. Apical segment of endosoma, *Cylindrostethus productus* Spinola.

457. Same, *Cylindrostethus erythropus* (Herrich-Schaeffer).

458. Same, *Cylindrostethus palmaris* Drake and Harris.

459. Same, *Cylindrostethus naiades* Kirkaldy.

FIGURES 447-459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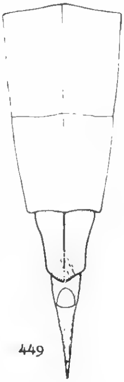
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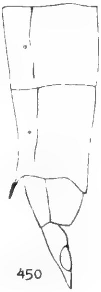
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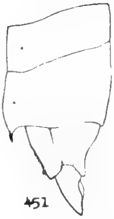
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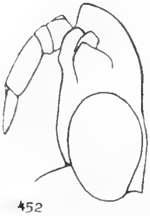
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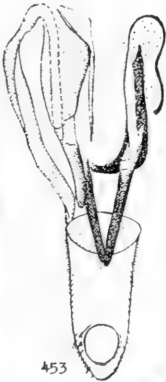
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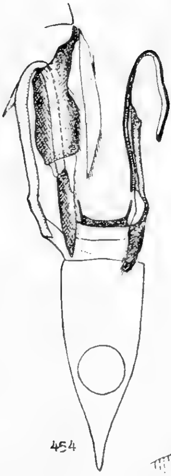
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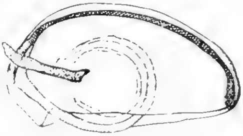
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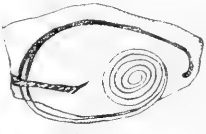
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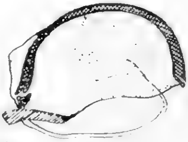
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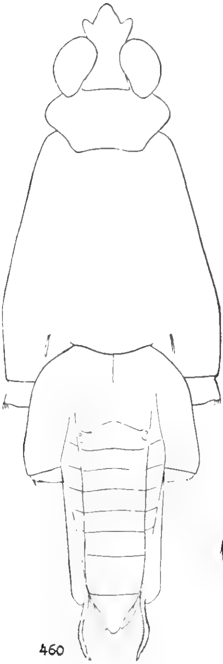
FIGURES 460-469

460. Dorsal view of wingless female, *Potamobates peruvianus* Hungerford.
461. Ventral view of metathorax, *Potamobates williamsi* Hungerford.
462. Lateral view of head, *Potamobates peruvianus* Hungerford.
463. Forewing, *Potamobates thomasi* Hungerford.
464. Hind wing, *Potamobates thomasi* Hungerford.
465. Female genitalia, *Potamobates peruvianus* Hungerford.
466. Antenna, *Potamobates peruvianus* Hungerford.
467. Front leg, *Potamobates peruvianus* Hungerford.
468. Middle tarsus, *Potamobates peruvianus* Hungerford.
469. Hind tarsus, *Potamobates peruvianus* Hungerford.

FIGURES 460-469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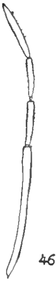
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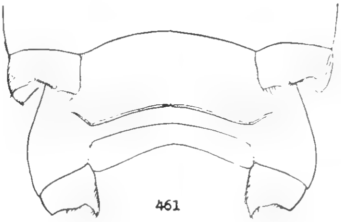
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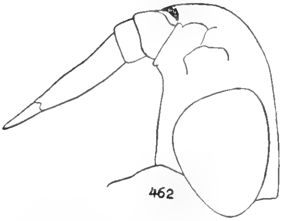
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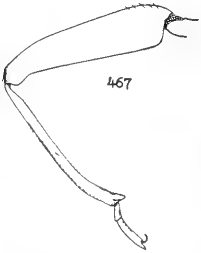
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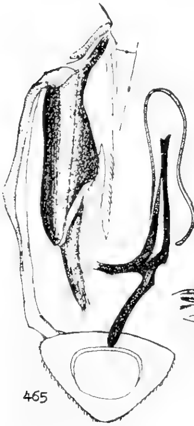
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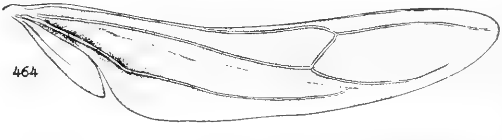
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FIGURES 470-480

470. Ventral view of female apical abdominal segments, *Potamobates thomasi* Hungerford.

471. Same, *Potamobates horváthi* Esaki.

472. Same, *Potamobates unidentatus* Champion.

473. Same, *Potamobates variabilis* Hungerford.

474. Lateral view of female apical abdominal segments, *Potamobates peruvianus* Hungerford.

475. Ventral view of male apical abdominal segments, *Potamobates thomasi* Hungerford.

476. Same, *Potamobates horváthi* Esaki.

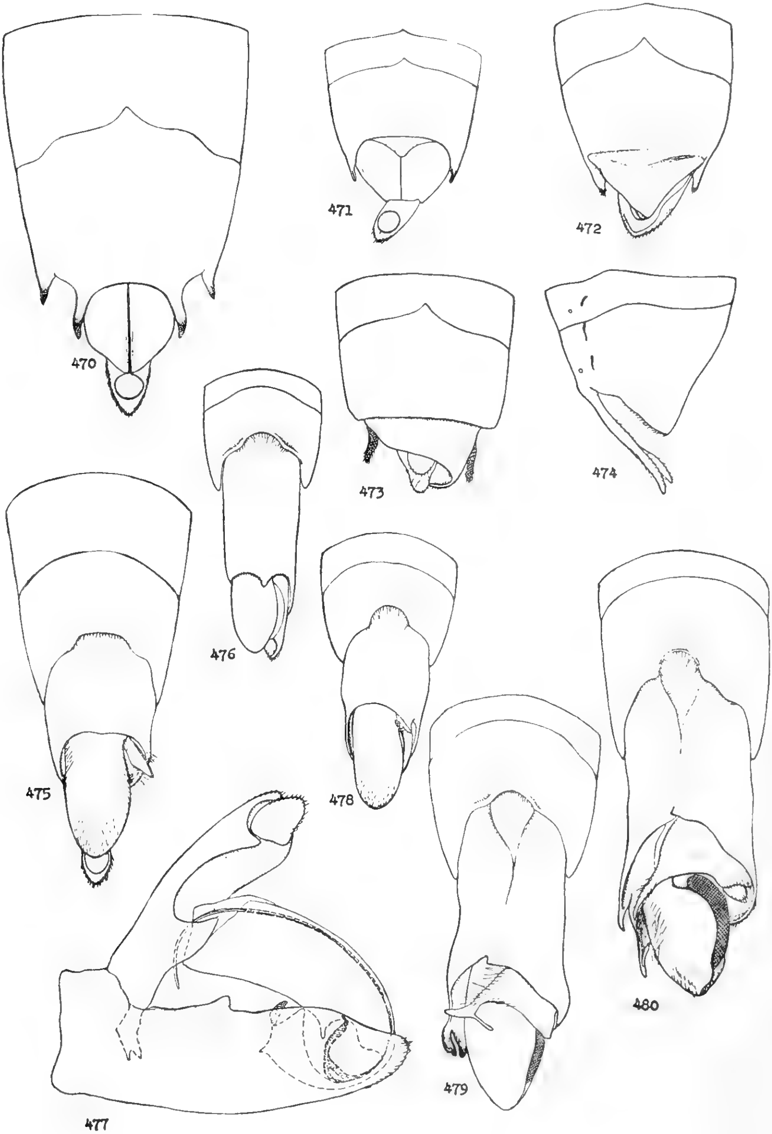
477. Lateral view of male genital segment, *Potamobates horváthi* Esaki.

478. Ventral view of male apical abdominal segments, *Potamobates unidentatus* Champion.

479. Same, *Potamobates variabilis* Hungerford.

480. Same, *Potamobates williamsi* Hungerford.

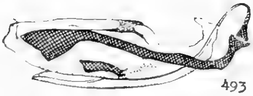
FIGURES 470-480



FIGURES 481-493

481. Dorsal view of wingless male *Platygerris depressus* B.-White.
482. Pronotum in winged form, *Platygerris asymmetricus* Hungerford.
483. Ventral view of male abdomen, *Platygerris asymmetricus* Hungerford.
484. Forewing, *Platygerris asymmetricus* Hungerford.
485. Hind wing, *Platygerris asymmetricus* Hungerford.
486. Lateral view of head, *Platygerris asymmetricus* Hungerford.
487. Antenna, *Platygerris asymmetricus* Hungerford.
488. Male front femur, *Platygerris asymmetricus* Hungerford.
489. Middle tibia and tarsus, *Platygerris asymmetricus* Hungerford.
490. Lateral view of male genital segment, *Potamobates williamsi* Hungerford.
491. Apical segment of endosoma, *Potamobates unidentatus* Champion.
492. Same, *Potamobates horváthi* Esaki.
493. Same, *Potamobates thomasi* Hungerford.

Figures 481-493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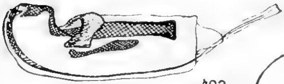
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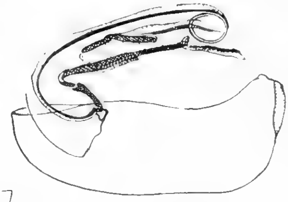
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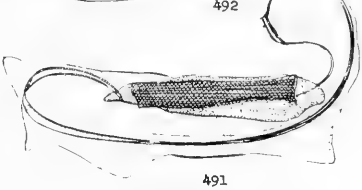
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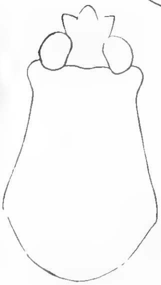
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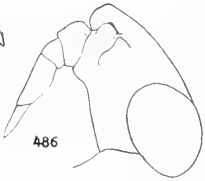
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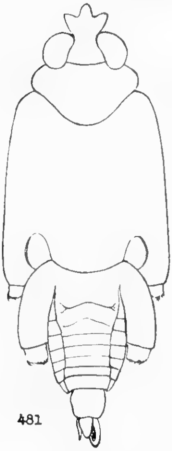
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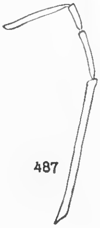
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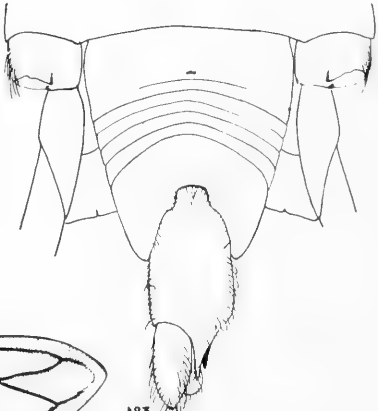
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FIGURES 494-504

494. Dorsal view of wingless female, *Platygerris asymmetricus* Hungerford.

495. Ventral view of male apical abdominal segments, *Platygerris asymmetricus* Champion.

496. Ventral view of male apical abdominal segments, *Platygerris caeruleus* Champion.

497. Ventral view of female apical abdominal segments, *Platygerris depressus* B.-White.

498. Ventral view of female apical abdominal segments, *Platygerris caeruleus* Champion.

499. Ventral view of female apical abdominal segments, *Platygerris asymmetricus* Hungerford.

500. Ventral view of female apical abdominal segments, *Platygerris asymmetricus* Hungerford.

501. Apical segment of endosoma, *Platygerris asymmetricus* Hungerford.

502. Female genitalia, *Platygerris asymmetricus* Hungerford.

503. Claws of front tarsus, *Platygerris caeruleus* Champion.

504. Last hind tarsal segment, *Platygerris asymmetricus* Hungerford.

FIGURES 494-504


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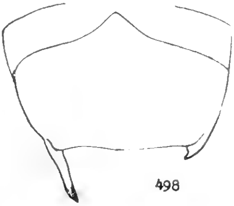
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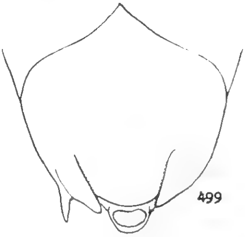
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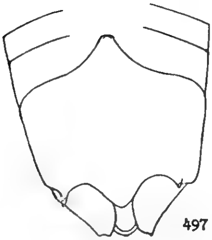
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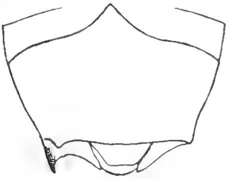
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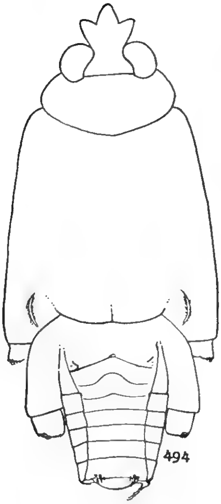
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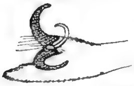
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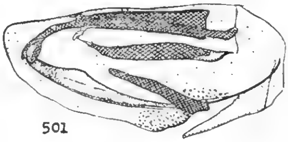
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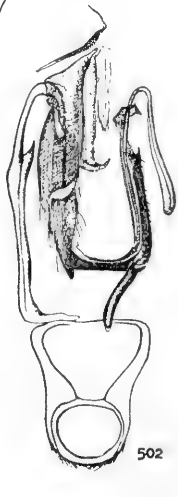
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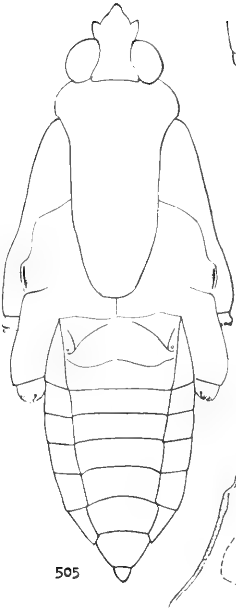
FIGURES 505-516

505. Dorsal view of wingless female, *Charmatometra bakeri* (Kirkaldy).
506. Lateral view of head, *Charmatometra bakeri* (Kirkaldy).
507. Ventral view of abdomen, *Charmatometra bakeri* (Kirkaldy).
508. Antenna, *Charmatometra bakeri* (Kirkaldy).
509. Male front leg, *Charmatometra bakeri* (Kirkaldy).
510. Apical part of male front femur, *Charmatometra bakeri* (Kirkaldy).
511. Last middle tarsal segment, *Charmatometra bakeri* (Kirkaldy).
512. Hind tarsus, *Charmatometra bakeri* (Kirkaldy).
513. Ventral view of male apical abdominal segments, *Charmatometra bakeri* (Kirkaldy).
514. Lateral view of male genital segment *Charmatometra bakeri* (Kirkaldy).
515. Apical segment of endosoma, *Charmatometra bakeri* (Kirkaldy).
516. Female genitalia, *Charmatometra bakeri* (Kirkaldy).

FIGURES 505-516



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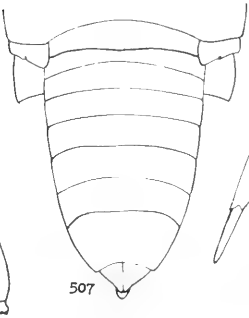

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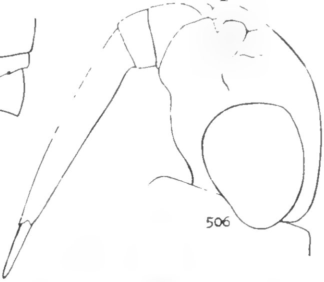

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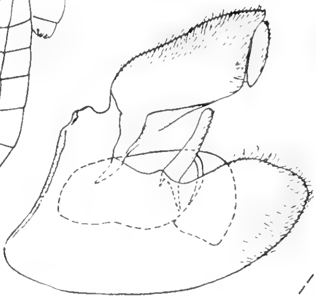

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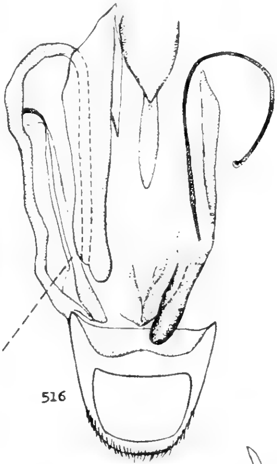

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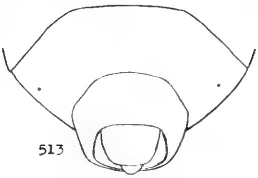

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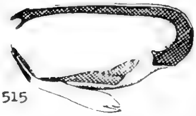

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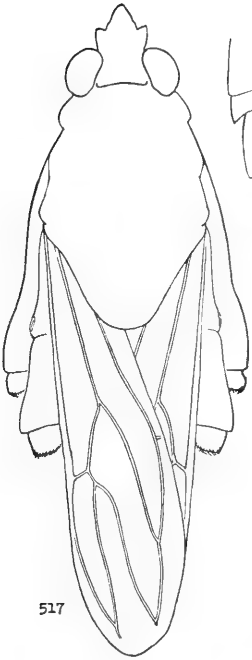
FIGURES 517-526

517. Dorsal view of winged female, *Eobates vittatus* (Shaw).
518. Dorsal view of wingless male, *Eobates vittatus* (Shaw).
519. Ventral view of male abdomen, *Eobates vittatus* (Shaw).
520. Lateral view of thorax, *Eobates vittatus* (Shaw).
521. Lateral view of head, *Eobates vittatus* (Shaw).
522. Antenna, *Eobates vittatus* (Shaw).
523. Male front leg, *Eobates vittatus* (Shaw).
524. Hind tarsus, *Eobates vittatus* (Shaw).
525. Ventral view of apical female abdomen, *Eobates vittatus* (Shaw).
526. Ventral view of male apical abdominal segments, *Eobates vittatus* (Shaw).

Figures 517-526



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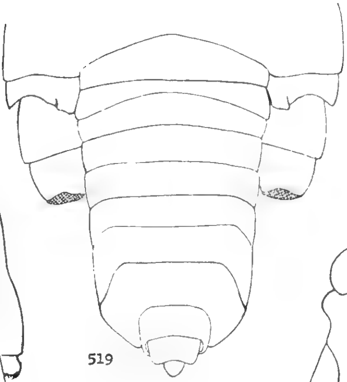

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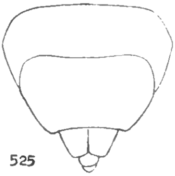

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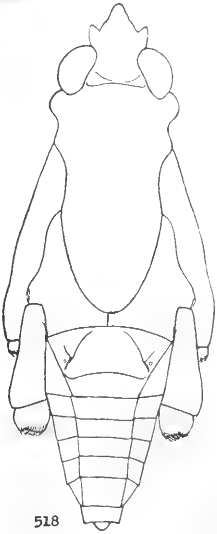

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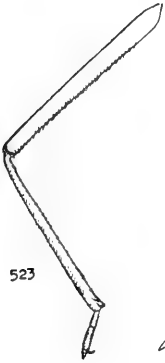

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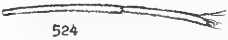

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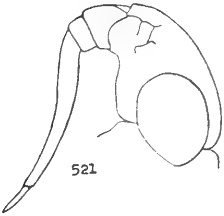

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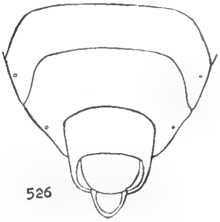

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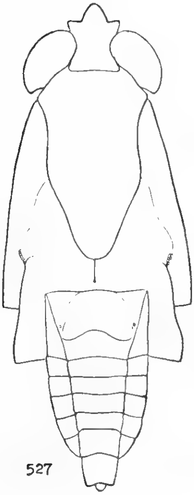
FIGURES 527-536

527. Dorsal view of wingless male, *Brachymetra lata* Shaw.
528. Dorsal view of thorax beneath wings, *Brachymetra lata* Shaw.
529. Lateral view of head, *Brachymetra shawi* Hungerford and Matsuda.
530. Forewing, *Brachymetra lata* Shaw.
531. Hind wing, *Brachymetra lata* Shaw.
532. Ventral view of metathorax and basal abdomen, *Brachymetra lata* Shaw.
533. Antenna, *Brachymetra shawi* Hungerford and Matsuda.
534. Male front leg, *Brachymetra shawi* Hungerford and Matsuda.
535. Last middle tarsal segment, *Brachymetra shawi* Hungerford and Matsuda.
536. Female genitalia, *Brachymetra lata* Shaw.

FIGURES 527-536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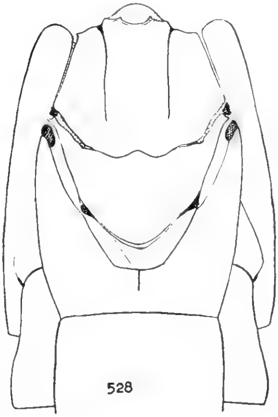
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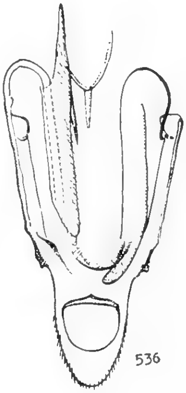
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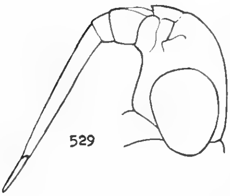
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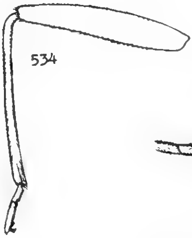
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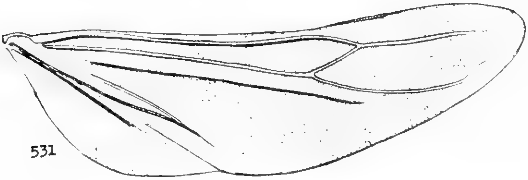
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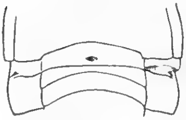
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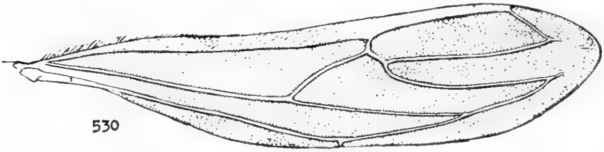
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FIGURES 537-547

537. Ventral view of female apical abdominal segments, *Brachymetra kleopatra* Kirkaldy.

538. Same, *Brachymetra anduzei* Drake and Harris.

539. Same, *Brachymetra lata* Shaw.

540. Same, *Brachymetra unca* Shaw.

541. Ventral view of male apical abdominal segments, *Brachymetra shawi* Hungerford and Matsuda.

542. Same, *Brachymetra anduzei* Drake and Harris.

543. Same, *Brachymetra lata* Shaw.

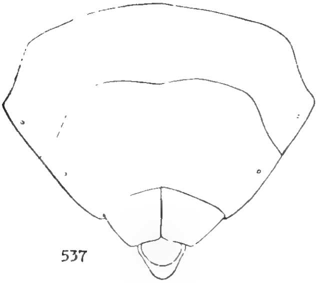
544. Apical segment of endosoma, *Brachymetra kleopatra* Kirkaldy.

545. Same, *Brachymetra lata* Shaw.

546. Same, *Brachymetra sp.* from Brazil.

547. Lateral view of male genital segment, *Brachymetra kleopatra* Kirkaldy.

FIGURES 537-547



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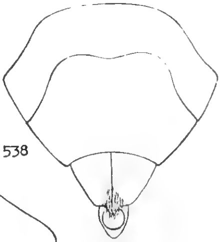

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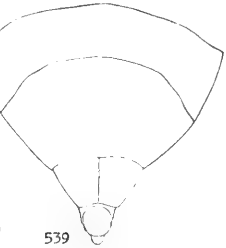

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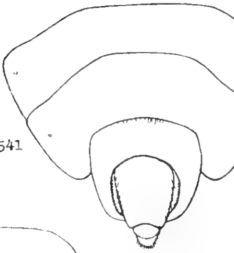

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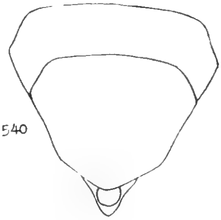

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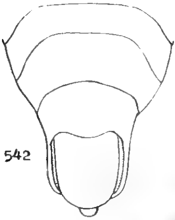

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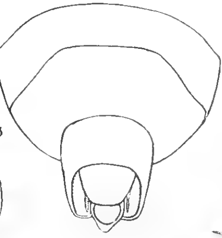

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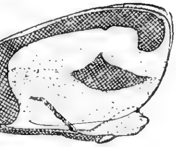

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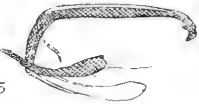

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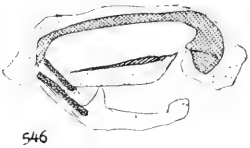

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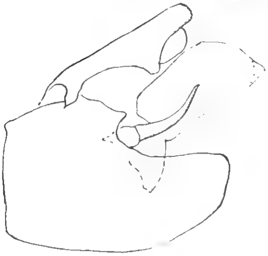

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Figures 548-558

548. Ventral view of winged male, *Eotrechus kalidasa* Kirkaldy.

549. Head and pronotum of winged male, *Eotrechus kalidasa* Kirkaldy.

550. Lateral view of head, *Eotrechus kalidasa* Kirkaldy.

551. Ventral view of male apical abdominal segments, *Eotrechus kalidasa* Kirkaldy.

552. Lateral view of male apical abdominal segments, *Eotrechus kalidasa* Kirkaldy.

553. Forewing, *Eotrechus kalidasa* Kirkaldy.

554. Hind wing, *Eotrechus kalidasa* Kirkaldy.

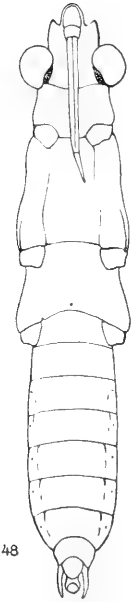
555. First and second antennal segments, *Eotrechus kalidasa* Kirkaldy.

556. Male front leg, *Eotrechus kalidasa* Kirkaldy.

557. Lateral view of male genital segment, *Eotrechus kalidasa* Kirkaldy.

558. Apical segment of endosoma, *Eotrechus kalidasa* Kirkaldy.

FIGURES 548-558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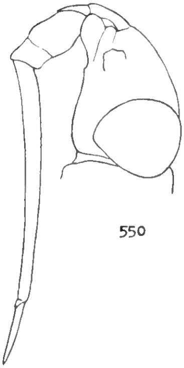
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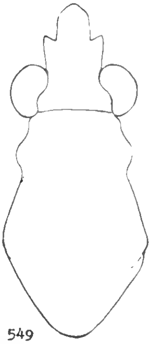
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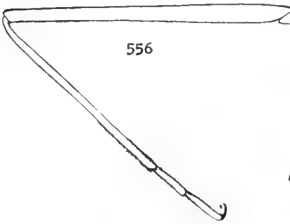
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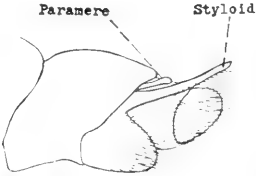

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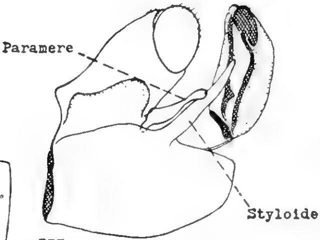

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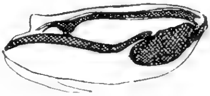
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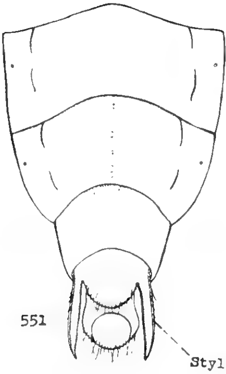

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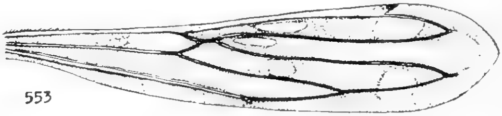
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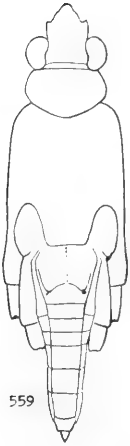
FIGURES 559-571

559. Dorsal view of wingless female, *Onychotrechus sakuntala* (Kirkaldy).
560. Ventral view of wingless female, *Onychotrechus sakuntala* (Kirkaldy).
561. Lateral view of head, *Onychotrechus sakuntala* (Kirkaldy).
562. Pronotum in winged form, *Onychotrechus sakuntala* (Kirkaldy).
563. Forewing, *Onychotrechus sakuntala* (Kirkaldy).
564. Hind wing, *Onychotrechus sakuntala* (Kirkaldy).
565. Antenna, *Onychotrechus sakuntala* (Kirkaldy).
566. Male front leg, *Onychotrechus sakuntala* (Kirkaldy).
567. Middle tarsus, *Onychotrechus sakuntala* (Kirkaldy).
568. Hind tarsus, *Onychotrechus sakuntala* (Kirkaldy).
569. Lateral view of male genital segment, *Onychotrechus sakuntala* (Kirkaldy).
570. Apical segment of endosoma, *Onychotrechus sakuntala* (Kirkaldy).
571. Female genitalia, *Onychotrechus sakuntala* (Kirkaldy).

FIGURES 559-571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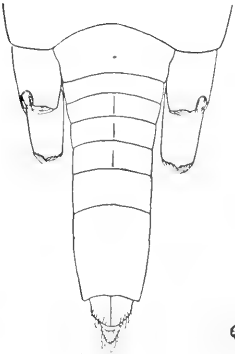
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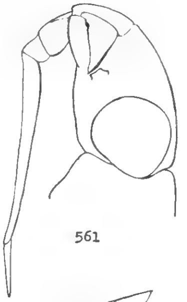
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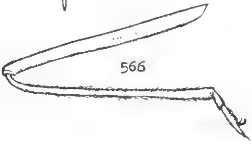
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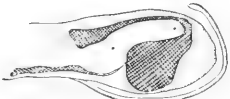
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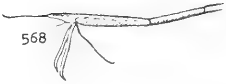
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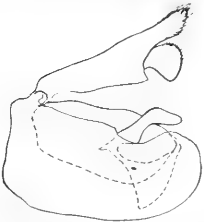
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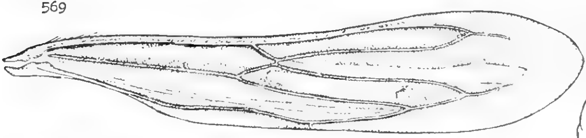
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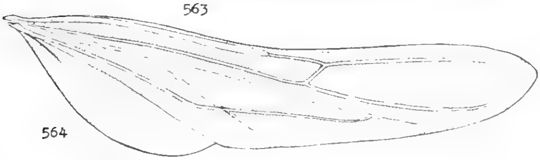
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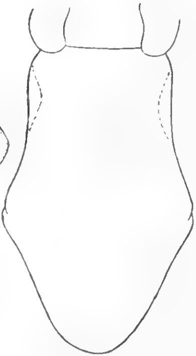
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FIGURES 572-583

572. Dorsal view of wingless male, *Chimarrhometra orientalis* (Distant).

573. Lateral view of head, *Chimarrhometra orientalis* (Distant).

574. Ventral view of male metathorax and abdomen, *Chimarrhometra orientalis* (Distant).

575. Male antenna, *Chimarrhometra orientalis* (Distant).

576. Lateral view of male genital segment, *Chimarrhometra orientalis* (Distant).

577. Male front leg, *Amemboa* sp. from Thailand.

578. Same, *Amemboa* sp. from Thailand.

579. Same, *Amemboa lyra* (paiva).

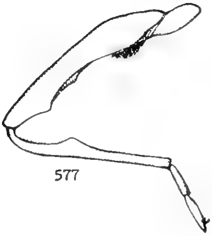
580. Same, *Chimarrhometra orientalis* (Distant).

581. Middle tarsus, *Chimarrhometra orientalis* (Distant).

582. Hind tarsus, *Chimarrhometra orientalis* (Distant).

583. Apical segment of endosoma, *Chimarrhometra orientalis* (Distant).

FIGURES 572-583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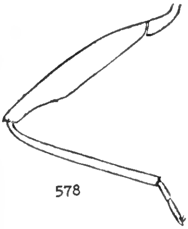
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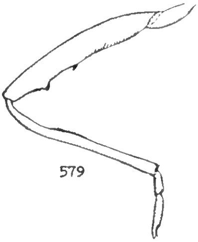
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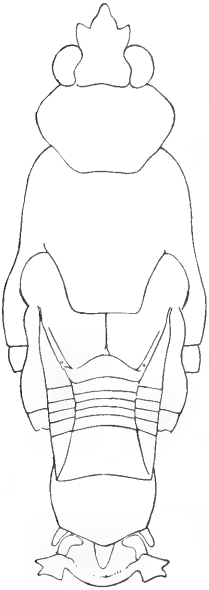
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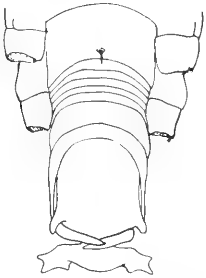
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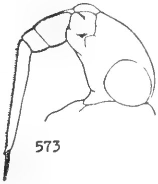
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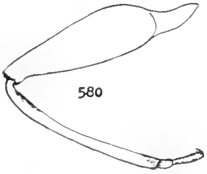
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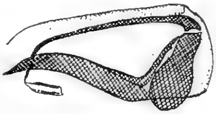
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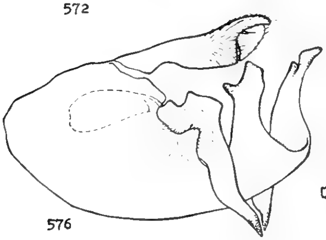
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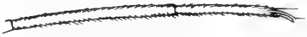
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FIGURES 584-597

584. Forewing, *Amemboa* sp. from Thailand.

585. Hind wing, *Amemboa* sp. from Thailand.

586. Pronotum in winged form, *Amemboa* sp. from Thailand.

587. Middle tarsus, *Amemboa horváthi* Esaki.

588. Hind tarsus, *Amemboa horváthi* Esaki.

589. Ventral view of male apical abdominal segments, *Amemboa* sp. from Thailand.

590. Ventral view of male apical abdominal segments, *Amemboa horváthi* Esaki.

591. Ventral view of male apical abdominal segments, *Amemboa fumi* Esaki.

592. Ventral view of male apical abdominal segments, *Amemboa lyra* (Paiva).

593. Ventral view of male apical abdominal segments, *Amemboa* sp. from Thailand.

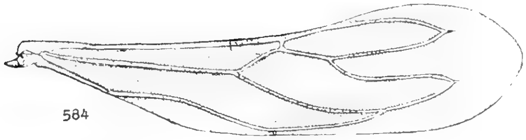
594. Lateral view of male genital segment, *Amemboa* sp. from Thailand.

595. Apical half of endosoma, *Amemboa* sp. from Thailand.

596. Same, *Amemboa lyra* (Paiva).

597. Female genitalia, *Amemboa lyra* (Paiva).

Figures 584-597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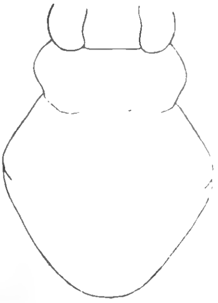
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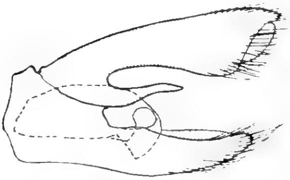
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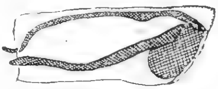
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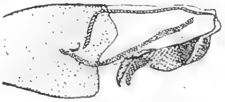
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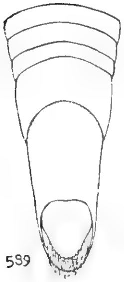
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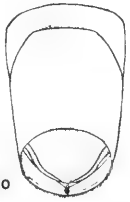
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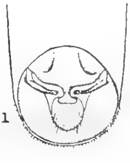
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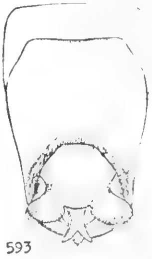
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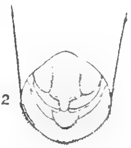
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Figures 598-608

598. Dorsal view of wingless male, *Amemboa fumi* Esaki.

599. Lateral view of thorax in winged form, *Onychotrechus sakuntala* (Kirkaldy).

600. Same, *Amemboa* sp. from Thailand.

601. Lateral view of head, *Amemboa horváthi* Esaki.

602. Ventral view of metathorax and abdomen, *Onychotrechus sakuntala* (Kirkaldy).

603. Ventral view of male abdomen, *Amemboa horváthi* Esaki.

604. Ventral view of female abdomen, *Amemboa horváthi* Esaki.

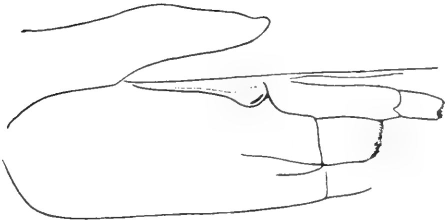
605. Male front leg, *Amemboa horváthi* Esaki.

606. Female front leg, *Amemboa horváthi* Esaki.

607. Lateral view of male genital segment, *Amemboa horváthi* Esaki.

608. Apical segment of endosoma, *Amemboa horváthi* Esaki.

Figures 598-608



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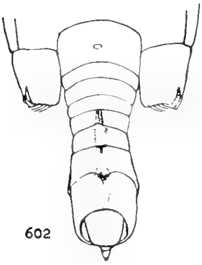

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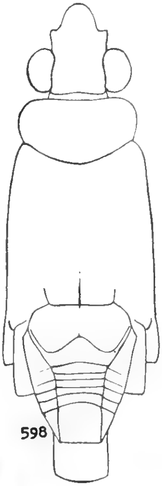

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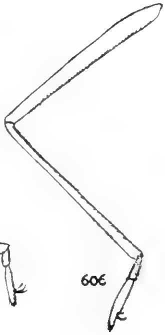

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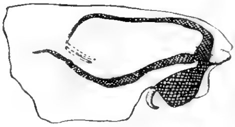

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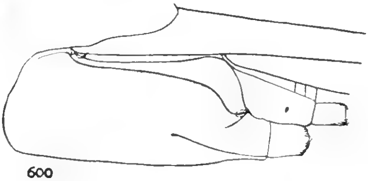

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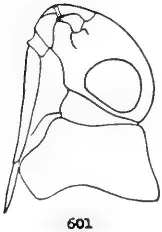

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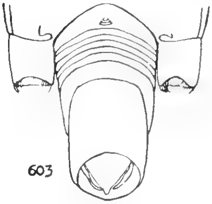

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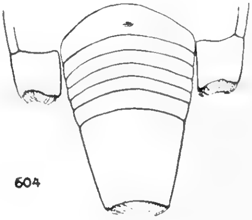

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FIGURES 609-619

609. Winged female, *Ptilomera (Proptilomera) himalayensis* Hungerford and Matsuda.

610. Wingless female, *Ptilomera (Ptilomera) dromas* Breddin.

611. Lateral view of head, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).

612. Forewing, *Ptilomera (Ptilomera)* sp. from Southern India.

613. Hind wing, *Ptilomera (Ptilomera)* sp. from Southern India.

614. Antenna, *Ptilomera (Proptilomera) himalayensis* Hungerford and Matsuda.

615. Male front leg, *Ptilomera (Proptilomera) himalayensis* Hungerford and Matsuda.

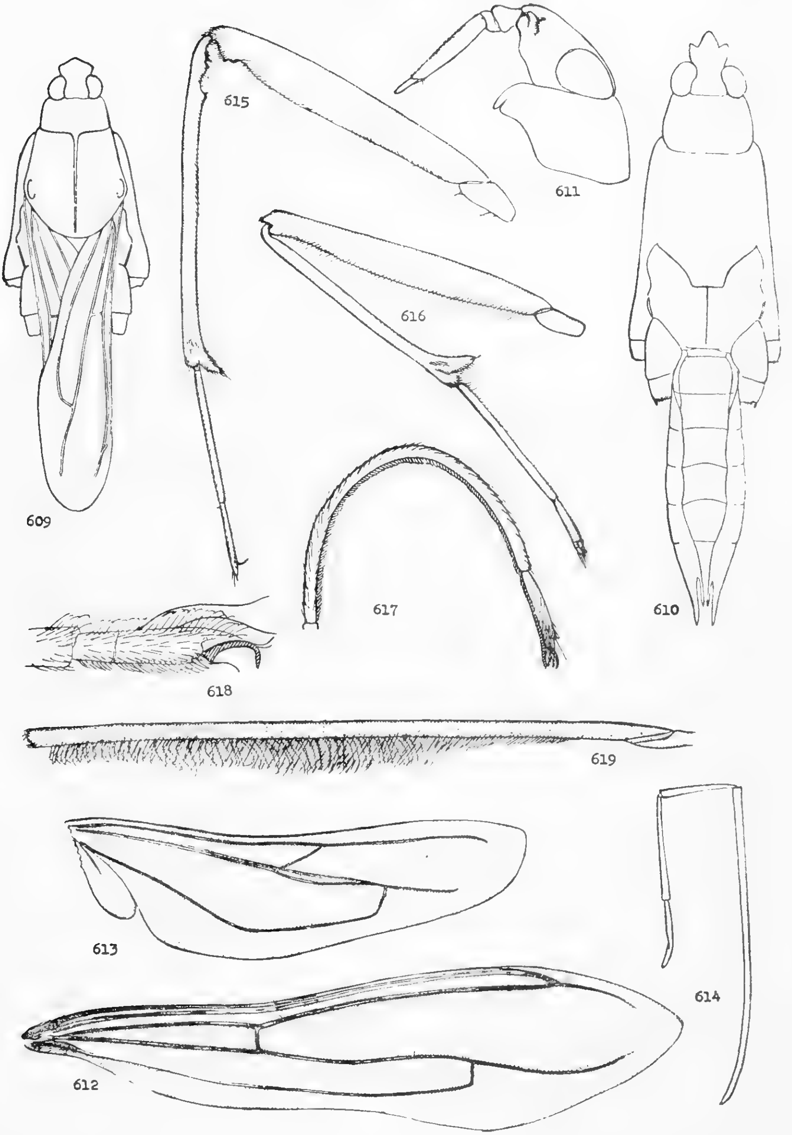
616. Female front leg, *Ptilomera (Ptilomera)* sp.

617. Hind tibia and tarsus, *Ptilomera (Ptilomera)* sp. from Southern India.

618. Hind tarsus, *Ptilomera (Ptilomera)* sp. from Southern India. Showing tarsal segmentation after treatment with KOH.

619. Middle femur, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).

FIGURES 609-619



FIGURES 620-629

620. Dorsal view of male apical abdominal segments, *Ptilomera (Proptilomera) himalayensis* Hungerford and Matsuda.

621. Same, *Ptilomera (Ptilomera) hylactor* Breddin.

622. Same, *Ptilomera (Ptilomera) dromas* Breddin.

623. Same, *Ptilomera (Ptilomera) pamphaga* Breddin.

624. Ventral view of male apical abdominal segments, *Ptilomera (Proptilomera) himalayensis* Hungerford and Matsuda.

625. Same, *Ptilomera (Ptilomera) pamphaga* Breddin.

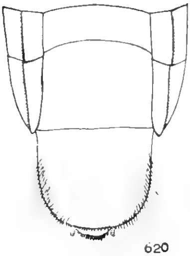
626. Dorsal view of male apical abdominal segments, *Ptilomera (Ptilomera) canace* Schmidt.

627. Same, *Ptilomera (Ptilomera) harpalus* Schmidt.

628. Same, *Ptilomera (Ptilomera) aëllo* Breddin.

629. Lateral view of male apical abdominal segments, *Ptilomera (Ptilomera) werneri* Hungerford and Matsuda.

FIGURES 620-629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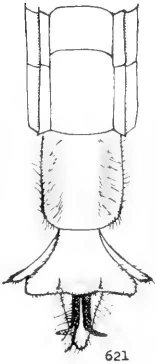
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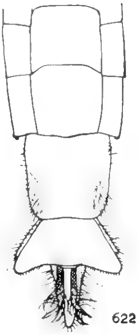
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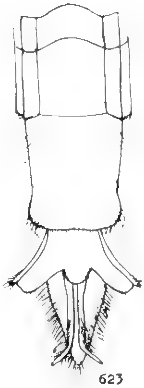
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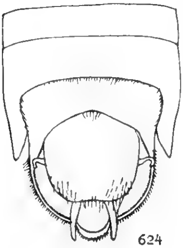
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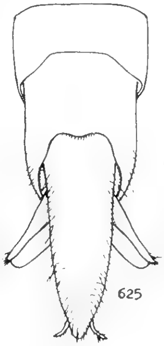
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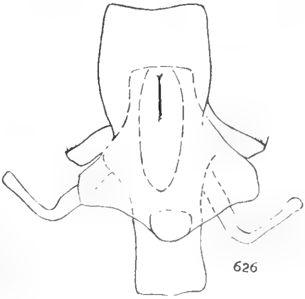
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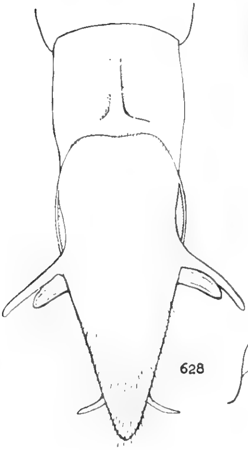
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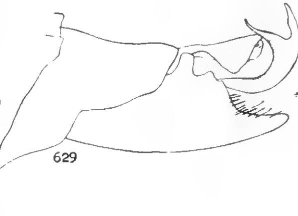
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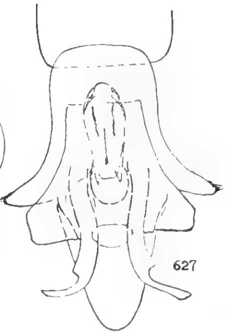
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FIGURES 630-641

630. Ventral view of metathorax and basal abdomen, *Ptilomera dromas* Breddin.

631. Lateral view of female apical abdominal segments, *Ptilomera (Proptilomera) himalayensis* Hungerford and Matsuda.

632. Same, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).

633. Dorsal view of female apical abdominal segments, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).

634. Lateral view of female apical abdominal segments, *Ptilomera (Ptilomera) hylactor* Breddin.

635. Same, *Ptilomera (Ptilomera) pamphaga* Breddin.

636. Lateral view of male genital segment, *Ptilomera (Ptilomera) himalayensis* Hungerford and Matsuda.

637. Same, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).

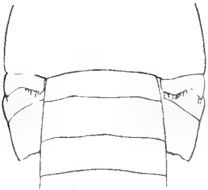
638. Apical segment of endosoma, *Ptilomera (Proptilomera) himalayensis* Hungerford and Matsuda.

639. Same, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).

640. Same, *Ptilomera (Ptilomera)* sp.

641. Female genitalia, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).

Figures 630-641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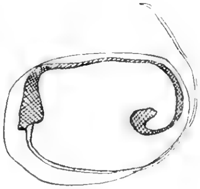
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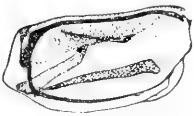
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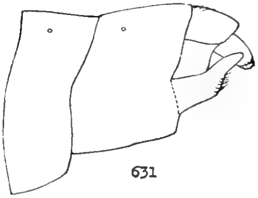
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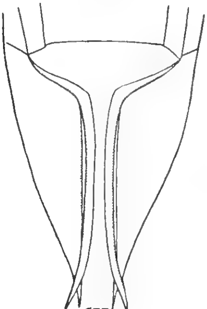
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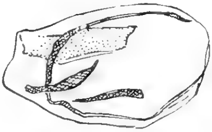
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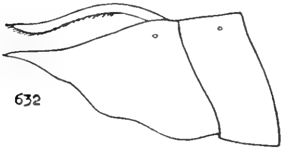
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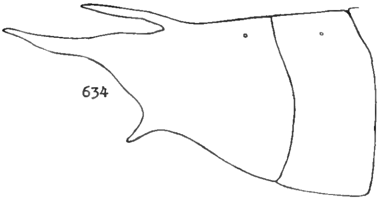
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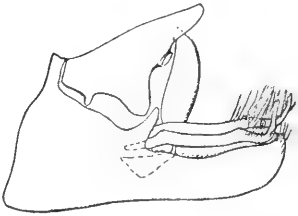
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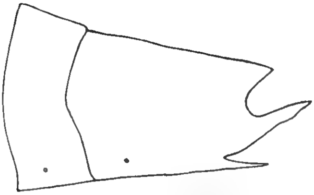
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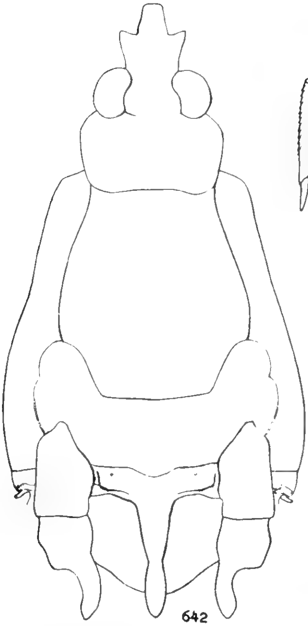
FIGURES 642-648

642. Dorsal view of wingless female, *Potamometra berezowskii* Bianchi.
643. Dorsal view of wingless male, *Potamometrta berezowskii* Bianchi.
644. Lateral view of head, *Potamometra berezowskii* Bianchi.
645. Forewing, *Potamometra berezowskii* Bianchi.
646. Hind wing, *Potamometra berezowskii* Bianchi.
647. Antenna, *Potamometra berezowskii* Bianchi.
648. Male front leg, *Potamometra berezowskii* Bianchi.

Figures 642-648



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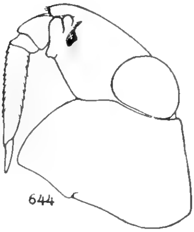

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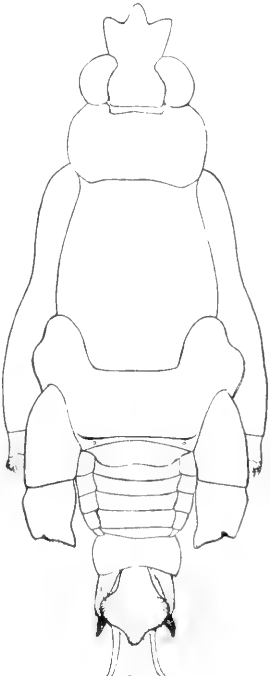

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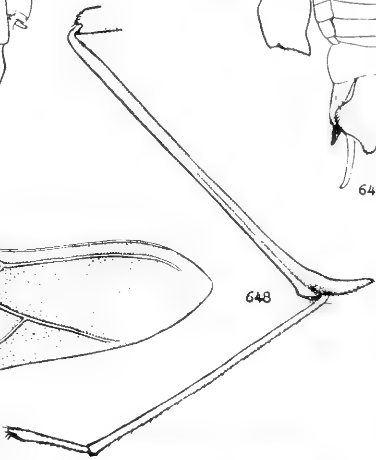

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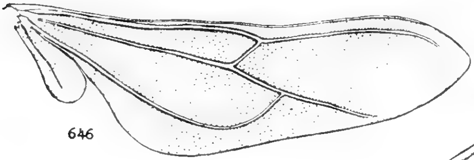

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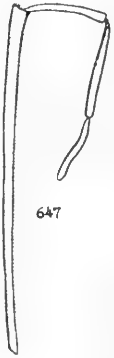

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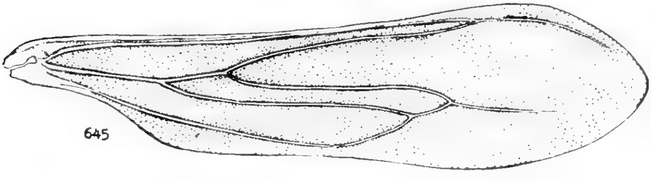

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FIGURES 649-655

649. Ventral view of female metathorax and abdomen, *Potamometra berezowskii* Bianchi.

650. Ventral view of male metathorax and abdomen, *Potamometra berezowskii* Bianchi.

651. Lateral view of male genital segment, *Potamometra berezowskii* Bianchi.

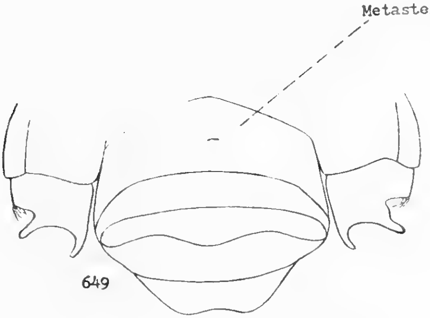
652. Apical segment of endosoma, *Potamometra berezowskii* Bianchi.

653. Female genitalia, *Potamometra berezowskii* Bianchi.

654. Last middle tarsal segment, *Potamometra berezowskii* Bianchi.

655. Hind tarsus, *Potamometra berezowskii* Bianchi.

Figures 649-655



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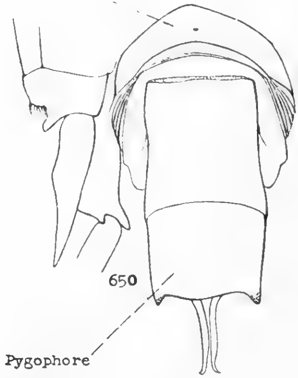

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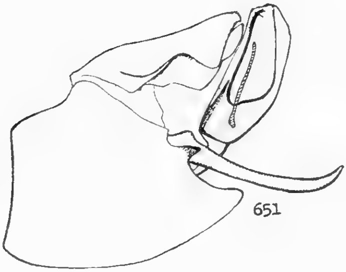

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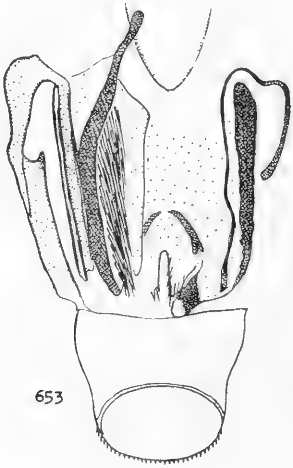

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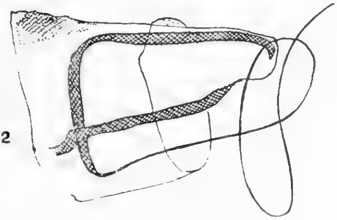

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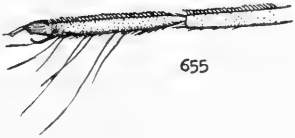

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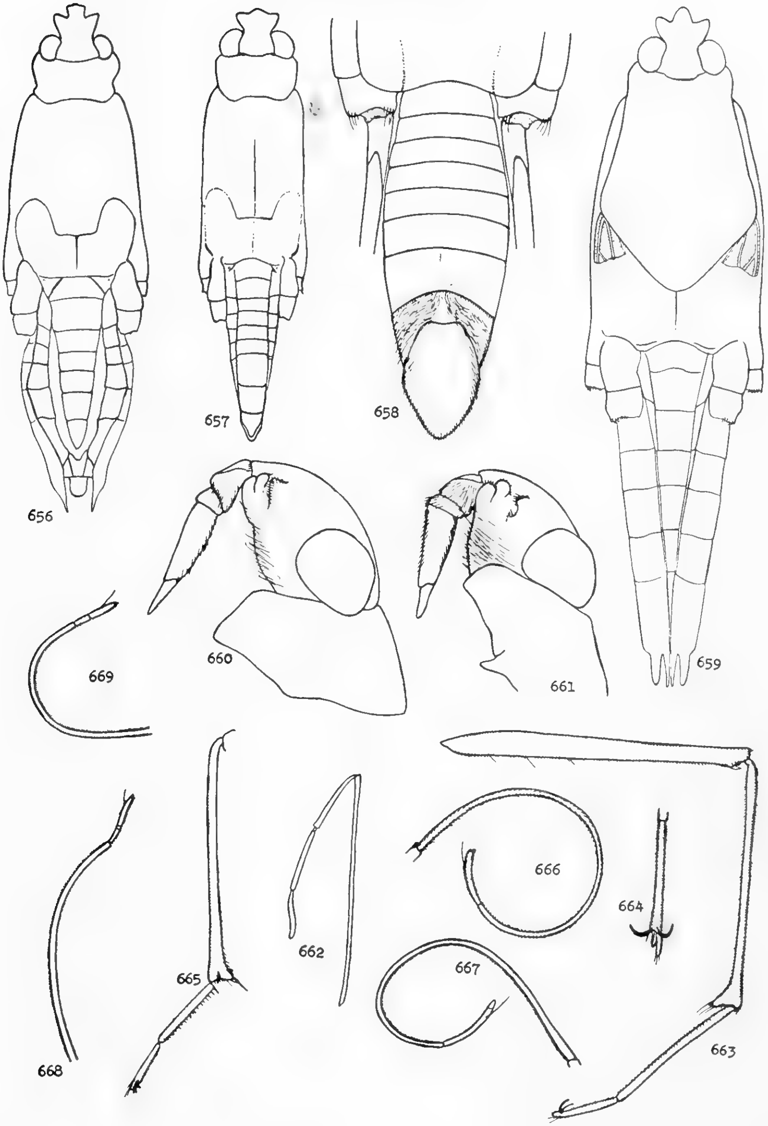
FIGURES 656-669

656. Dorsal view of wingless female, *Rhyacobates takahashii* Esaki.
657. Dorsal view of wingless male, *Rhyacobates takahashii* Easki.
658. Ventral view of abdomen, *Rhyacobates takahashii* Esaki.
659. Dorsal view of winged female, *Rhyacobates lundbladi* (Hungerford).
660. Lateral view of head, *Rhyacobates takahashii* Esaki.
661. Lateral view of head, *Rhyacobates lundbladi* (Hungerford).
662. Antenna, *Rhyacobates takahashii* Esaki.
663. Female front leg, *Rhyacobates takahashii* Esaki.
664. Second front tarsal segment, *Rhyacobates takasashii* Esaki.
665. Male front tibia and tarsus, *Rhyacobates lundbladi* (Hungerford).
666. Middle tarsus, *Rhyacobates takahashii* Esaki.
667. Middle tarsus, *Rhyacobates lundbladi* (Hungerford).
668. Hind tibia and tarsus, *Rhyacobates takahashii* Esaki.
669. Hind tibia and tarsus, *Rhyacobates lundbladi* (Hungerford).

Figures 656-669



FIGURES 670-680

670. Antenna, *Rhyacobates lundbladi* (Hungerford).

671. Lateral view of male apical abdominal segments, *Rhyacobates lundbladi* (Hungerford).

672. Ventral view of apical male abdominal segments, *Rhyacobates lundbladi* (Hungerford).

673. Lateral view of female apical abdominal segments, *Rhyacobates chinensis* Hungerford and Matsuda.

674. Lateral view of male genital segment, *Rhyacobates takahashii* Esaki.

675. Ventral view of female apical abdominal segments, *Rhyacobates takahashii* Esaki.

676. Lateral view of female apical abdominal segments, *Rhyacobates takahashii* Esaki.

677. Apical segment of endosoma, *Rhyacobates lundbladi* (Hungerford).

678. Apical segment of endosoma, *Rhyacobates takahashii* Esaki.

679. Lateral view of male genital segment, *Rhyacobates lundbladi* (Hungerford).

680. Female genitalia, *Rhyacobates lundbladi* (Hungerford).

FIGURES 670-680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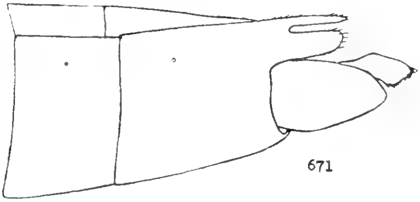
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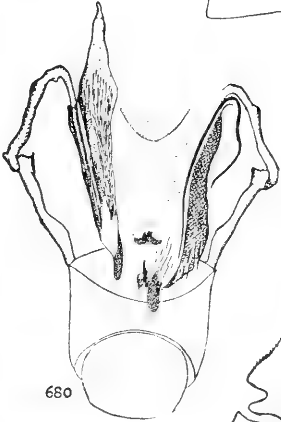
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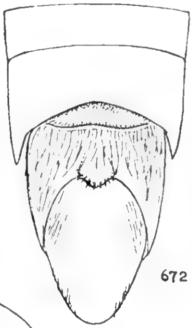
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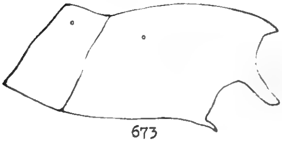
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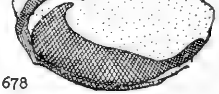
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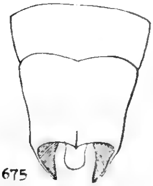
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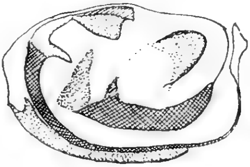
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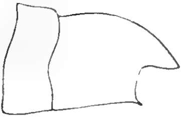
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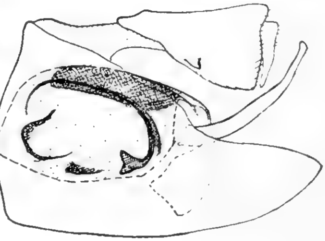
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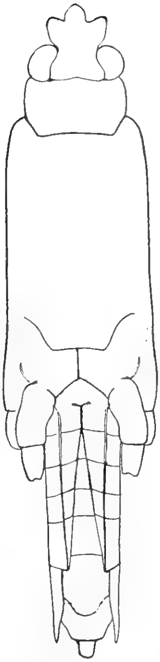
FIGURES 681-691

681. Dorsal view of wingless female, *Heterobates dohrandti* Bianchi.
682. Dorsal view of wingless male, *Heterobates dohrandti* Bianchi.
683. Dorsal view of wingless female, *Heterobates bilobatus* (Esaki).
684. Ventral view of wingless female, *Heterobates dohrandti* Bianchi.
685. Lateral view of apical abdominal segments in wingless female, *Heterobates dohrandti* Bianchi.
686. Antenna, *Heterobates dohrandti* Bianchi.
687. Antenna, *Heterobates bilobatus* (Esaki).
688. Lateral view of head, *Heterobates bilobatus* (Esaki).
689. Middle tarsus, *Heterobates dohrandti* Bianchi.
690. Hind tibia and tarsus, *Heterobates dohrandti* Bianchi.
691. Ventral view of male metathorax and basal abdomen, *Heterobates dohrandti* Bianchi.

FIGURES 681-691



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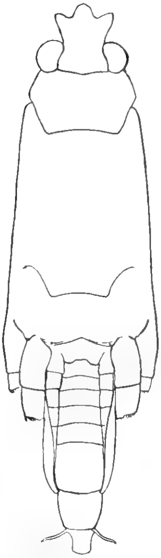

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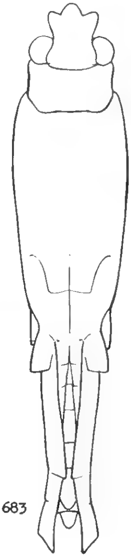

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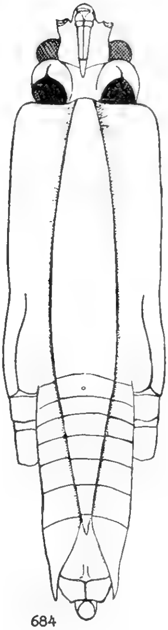

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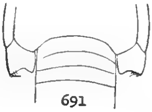

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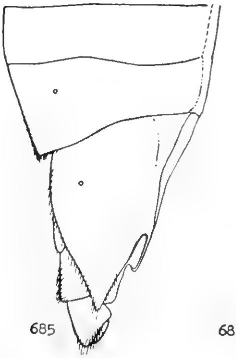

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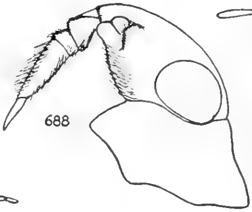

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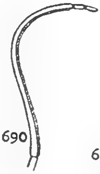

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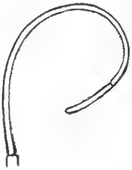

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FIGURES 692-701

692. Male front leg, *Heterobates dohrandti* Bianchi.

693. Female front leg, *Heterobates bilobatus* (Esaki).

694. Ventral view of male apical abdominal segments, *Heterobates dohrandti* Bianchi.

695. Lateral view of male genital segment, *Heterobates dohrandti* Bianchi.

696. Apical segment of endosoma, *Heterobates dohrandti* Bianchi.

697. Ventral view of female apical abdominal segments, *Heterobates dohrandti* Bianchi.

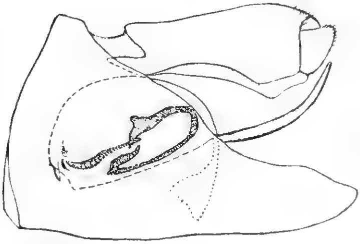
698. Female genitalia, *Heterobates dohrandti* Bianchi.

699. Lateral view of female apical abdominal segments, *Heterobates bilobatus* (Esaki).

700. Ventral view of female apical abdominal segments, *Heterobates bilobatus* (Esaki).

701. Lateral view of head, *Heterobates dohrandti* Bianchi.

FIGURES 692-701



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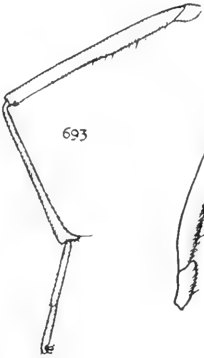

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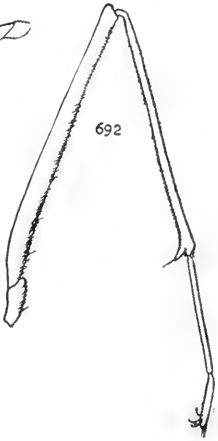

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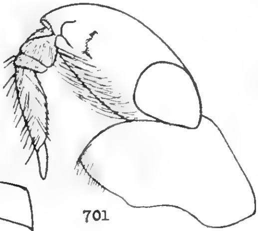

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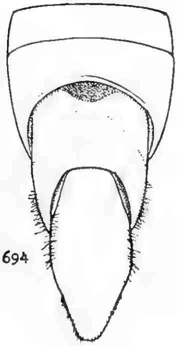

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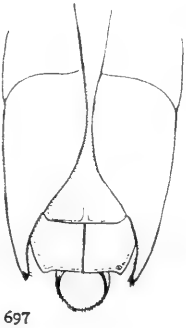

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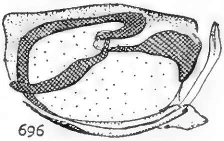

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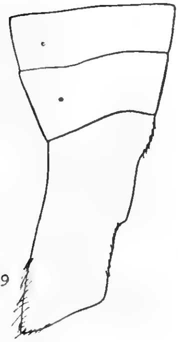

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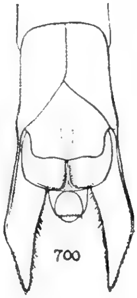

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FIGURES 702-712

702. Dorsal view of wingless female, *Potamometroides madagascariensis* Hungerford.

703. Dorsal view of wingless male, *Potamometroides madagascariensis* Hungerford.

704. Ventral view of male abdomen, *Potamometroides madagascariensis* Hungerford.

705. Lateral view of head, *Potamometroides madagascariensis* Hungerford.

706. Female antenna, *Potamometroides madagascariensis* Hungerford.

707. Lateral view of male genital segment, *Potamometroides madagascariensis* Hungerford.

708. Apical segment of endosoma, *Potamometroides madagascariensis* Hungerford.

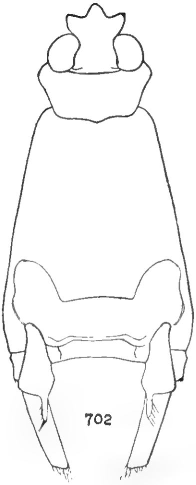
709. Female genitalia, *Potamometroides madagascariensis* Hungerford.

710. Female front leg, *Potamometroides madagascariensis* Hungerford.

711. Male hind tibia and tarsus, *Potamometroides madagascariensis* Hungerford.

712. Middle tarsus, *Potamometroides madagascariensis* Hungerford.

FIGURES 702-712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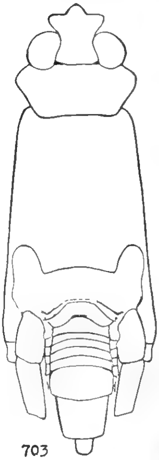
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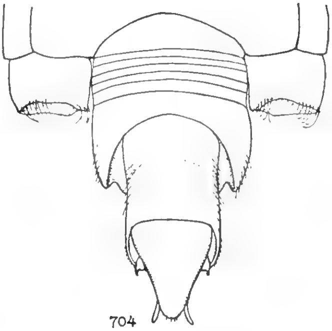
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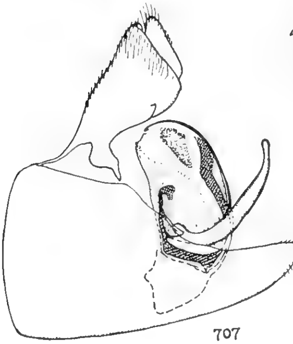
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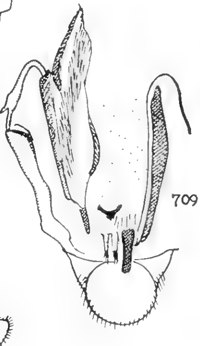
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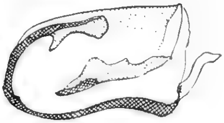
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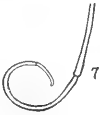
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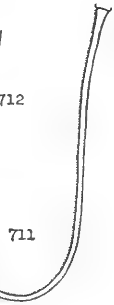
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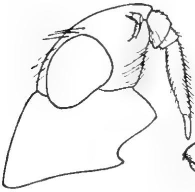
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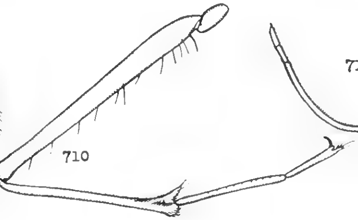
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FIGURES 713-721

713. Dorsal view of wingless female, *Potamometropsis hoogstraali* Hungerford.

714. Dorsal view of wingless female, *Potamometropsis werneri* Hungerford.

715. Lateral view of head, *Potamometropsis hoogstraali* Hungerford.

716. Female front leg, *Potamometropsis hoogstraali* Hungerford.

717. Male front leg, *Potamometropsis hoogstraali* Hungerford.

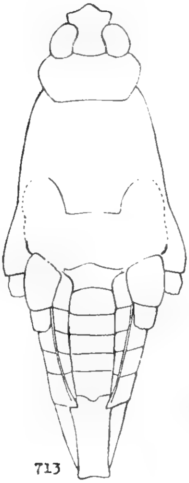
718. Hind tibia and tarsus, *Potamometropsis werneri* Hungerford.

719. Middle tarsus, *Potamometropsis werneri* Hungerford.

720. Lateral view of male genital segment, *Potamometropsis hoogstraali* Hungerford.

721. Female genitalia, *Potamometropsis hoogstraali* Hungerford.

FIGURES 713-721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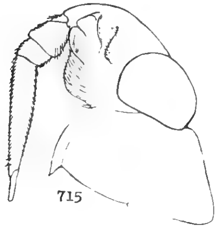
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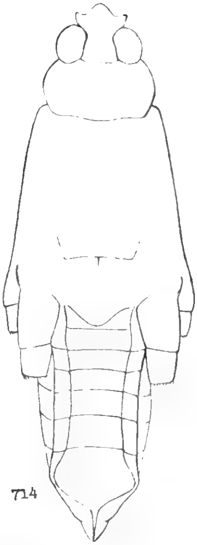
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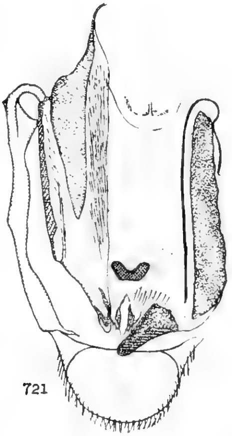
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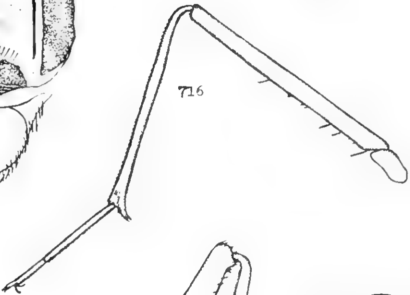
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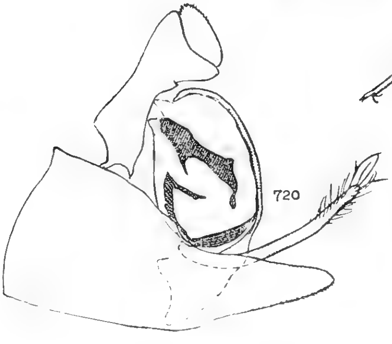
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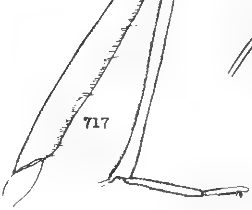
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FIGURES 722-735

722. Ventral view of male apical abdominal segments, *Potamometropsis obnubila* Lundblad.

723. Dorsal view of male apical abdominal segments, *Potamometropsis obnubila* Lundblad.

724. Ventral view of male apical abdominal segments, *Potamometropsis werneri* Hungerford.

725. Dorsal view of male apical abdominal segments, *Potamometropsis werneri* Hungerford.

726. Lateral view of female apical abdominal segments, *Potamometropsis werneri* Hungerford.

727. Ventral view of male apical abdominal segments, *Potamometropsis hoogstraali* Hungerford.

728. Dorsal view of male apical abdominal segments, *Potamometropsis hoogstraali* Hungerford.

729. Apical segment of endosoma, *Potamometropsis hoogstraali* Hungerford.

730. Lateral view of female apical abdominal segments, *Potamometropsis hoogstraali* Hungerford.

731. Lateral view of female apical abdominal segments, *Potamometropsis obnubila* Lundblad.

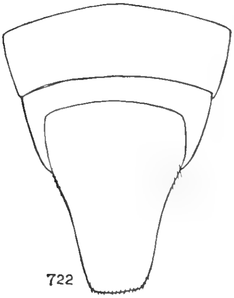
732. Ventral view of male apical abdominal segments, *Rheumatogonus intermedius* Hungerford.

733. Ventral view of female apical abdominal segments, *Rheumatogonus intermedius* Hungerford.

734. Ventral view of male apical abdominal segments, *Rheumatogonus burmanus* (Distant).

735. Ventral view of female apical abdominal segments, *Rheumatogonus burmanus* (Distant).

Figures 722-735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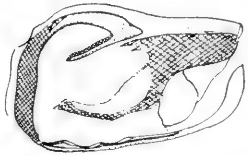
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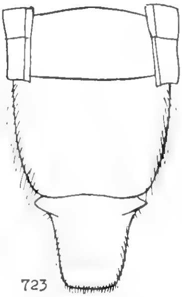
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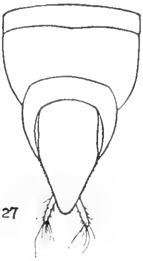
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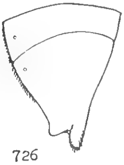
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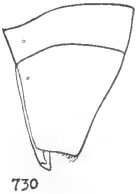
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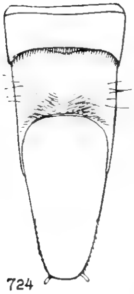
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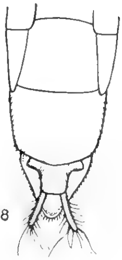
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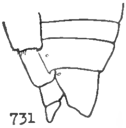
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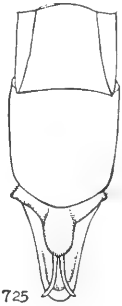
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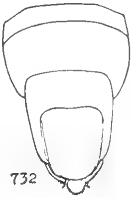
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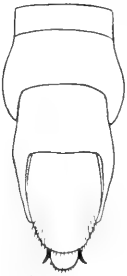
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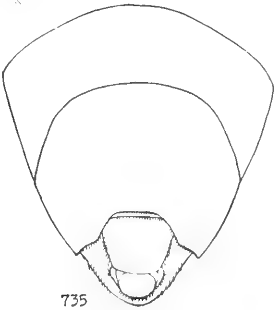
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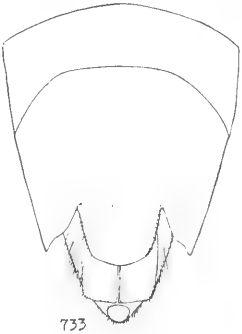
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FIGURES 736-747

736. Dorsal view of wingless male, *Rheumatogonus intermedius* Hungerford.

737. Ventral view of male abdomen, *Rheumatogonus intermedius* Hungerford.

738. Lateral view of head, *Rheumatogonus intermedius* Hungerford.

739. Antenna, *Rheumatogonus intermedius* Hungerford.

740. Forewing, *Rheumatogonus intermedius* Hungerford.

741. Hind wing, *Rheumatogonus intermedius* Hungerford.

742. Male front leg, *Rheumatogonus intermedius* Hungerford.

743. Lateral view of male genital segment, *Rheumatogonus intermedius* Hungerford.

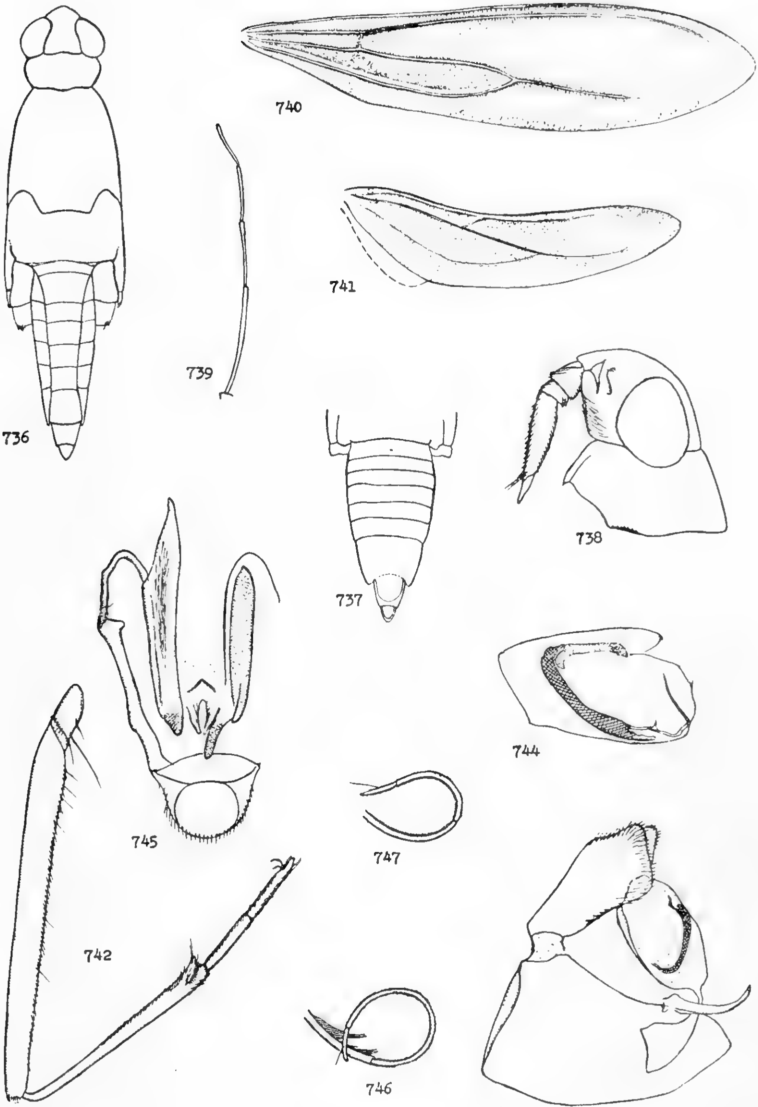
744. Apical segment of endosoma, *Rheumatogonus intermedius* Hungerford.

745. Female genitalia, *Rheumatogonus intermedius* Hungerford.

746. Middle tarsus, *Rheumatogonus intermedius* Hungerford.

747. Hind tarsus, *Rheumatogonus intermedius* Hungerford. Incorrectly drawn, see description.

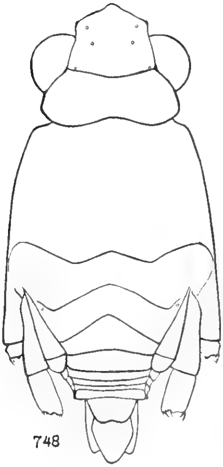
FIGURES 736-747



FIGURES 748-759

748. Dorsal view of wingless male, *Asclepios apicalis* Esaki.
749. Ventral view of head, *Asclepios apicalis* Esaki.
750. Lateral view of head, *Asclepios apicalis* Esaki.
751. Ventral view of male abdomen, *Asclepios apicalis* Esaki.
752. Antenna, *Asclepios coreanus* Esaki.
753. Male front leg, *Asclepios coreanus* Esaki.
754. Female front leg, *Asclepios coreanus* Esaki.
755. Lateral view of male apical abdominal segments, *Asclepios coreanus* Esaki.
756. Ventral view of female abdomen, *Asclepios coreanus miyamotoi* Esaki.
757. Last middle tarsal segment, *Asclepios coreanus miyamotoi* Esaki.
758. Hind tarsus, *Asclepios apicalis* Esaki.
759. Female genitalia, *Asclepios coreanus miyamotoi* Esaki.

Figures 748-759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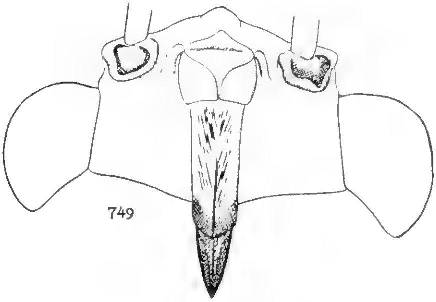
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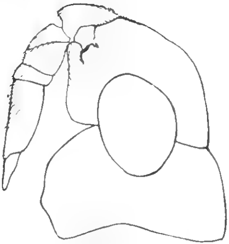
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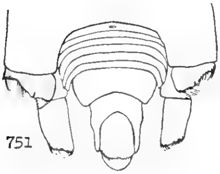
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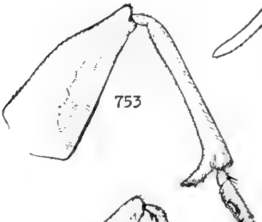
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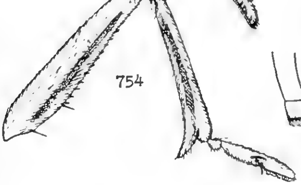
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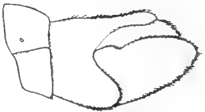
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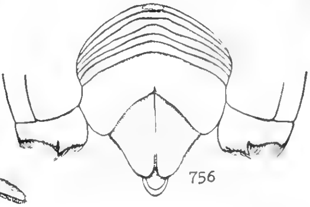
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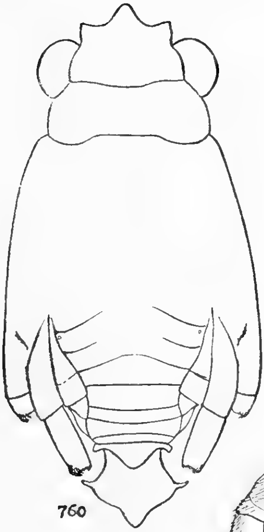
FIGURES 760-766

760. Dorsal view of male, *Halobates sobrinus* B.-White.
761. Dorsal view of female, *Halobates sobrinus* B.-White.
762. Nymph, *Halobates sobrinus* B.-White.
763. Lateral view of head, *Halobates hawaiiensis* Usinger.
764. Front tibia and tarsus, *Halobates sobrinus* B.-White.
765. Lateral view of male genital segment, *Asclepios coreanus* Esaki.
766. Apical segment of endosoma, *Asclepios coreanus* Esaki.

FIGURES 760-766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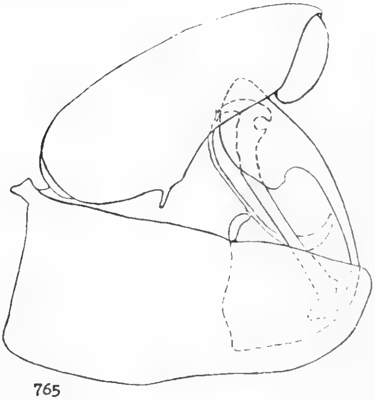
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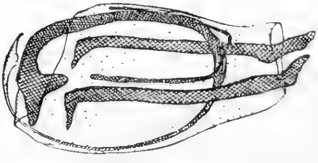
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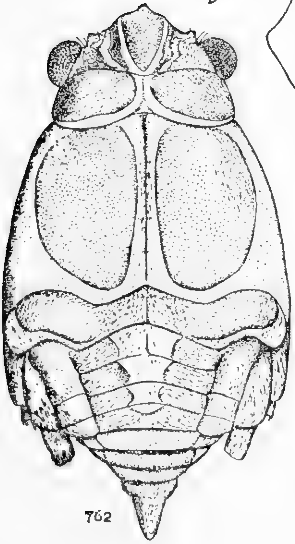
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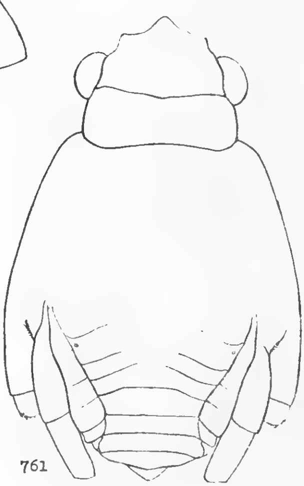
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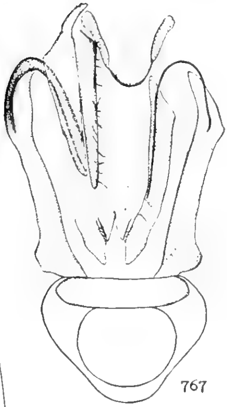
FIGURES 767-776

767. Female genitalia, *Halobates sobrinus* B.-White.
768. Female antenna, *Halobates sobrinus* B.-White.
769. Middle tarsus, *Halobates sobrinus* B.-White.
770. Ventral view of female abdomen, *Halobates micans* Eschscholtz.
771. Ventral view of female abdomen, *Halobates hawaiiensis* Usinger.
772. Lateral view of male abdomen, *Halobates hawaiiensis* Usinger.
773. Ventral view of abdomen, *Halobates hawaiiensis* Usinger.
774. Ventral view of male abdomen, *Halobates mariannarum* Esaki.
775. Ventral view of male abdomen, *Halobates sobrinus* B.-White.
776. Hind tarsus, *Halobates sobrinus* B.-White.

FIGURES 767-776

769



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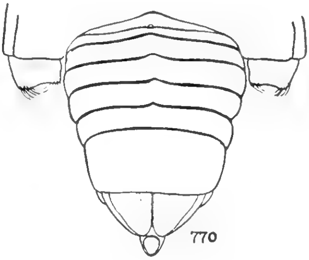

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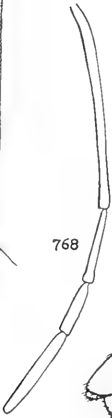

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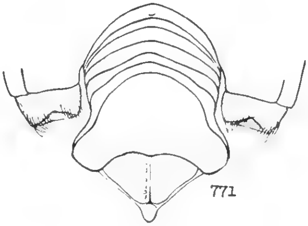

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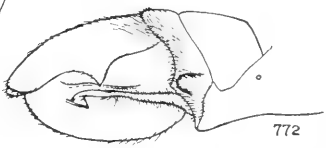

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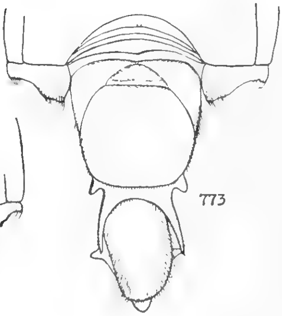

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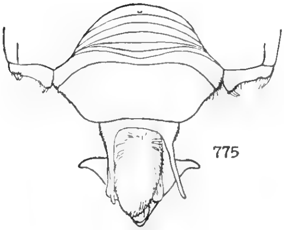

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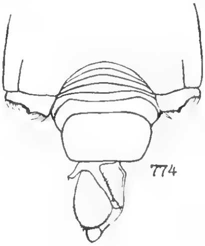

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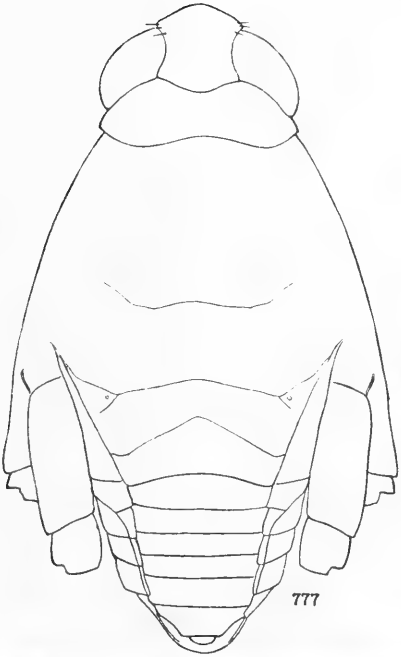
FIGURES 777-784

777. Dorsal view of wingless female, *Metrocoris histrio* (B.-White).
778. Lateral view of head, *Metrocoris histrio* (B.-White).
779. Forewing, *Metrocoris* sp. from the Philippines.
780. Hind wing, *Metrocoris* sp. from the Philippines.
781. Front tarsus, *Metrocoris strangulator* Breddin.
782. Male antenna, *Metrocoris histrio* (B.-White).
783. Middle last tarsal segment, *Metrocoris strangulator* Breddin.
784. Hind tarsus, *Metrocoris strangulator* Breddin.

Figures 777-784



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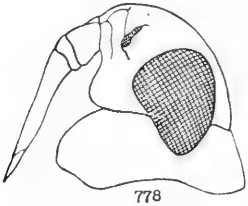

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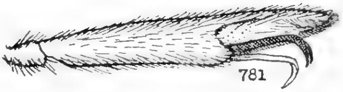

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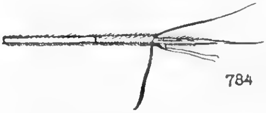

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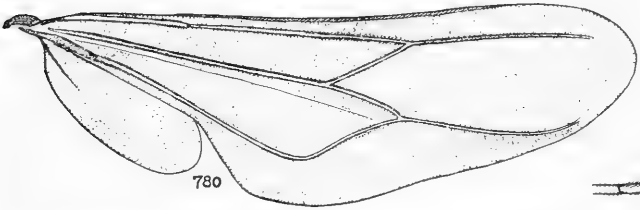

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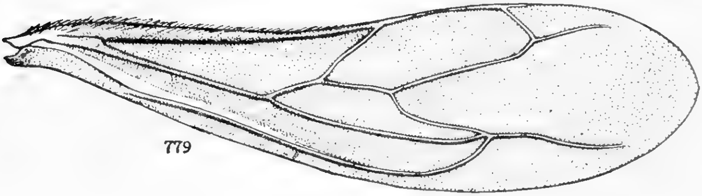

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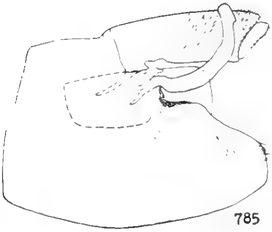
FIGURES 785-796

785. Lateral view of male genital segment, *Metrocoris ståli* (Dohrn). (?)
786. Apical segment of endosoma, *Metrocoris ståli* (Dohrn). (?)
787. Ventral view of female abdomen, *Metrocoris histrio* (B.-White).
788. Ventral view of female abdomen, *Metrocoris strangulator* Breddin.
789. Ventral view of male abdomen, *Metrocoris ståli* (Dohrn). (?)
790. Ventral view of female abdomen, *Metrocoris ståli* (Dohrn). (?)
791. Ventral view of male abdomen, *Metrocoris histrio* (B.-White).
792. Ventral view of male abdomen, *Metrocoris strangulator* Breddin.
793. Ventral view of male abdomen, *Metrocoris* sp. from Nepal.
794. Male front leg, *Metrocoris histrio* (B.-White).
795. Male front leg, *Metrocoris strangulator* Breddin.
796. Female genitalia, *Metrocoris* sp. from India.

FIGURES 785-796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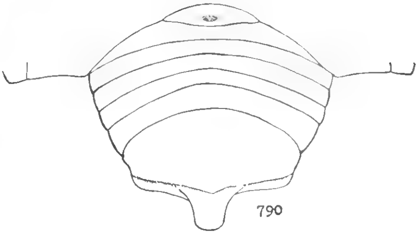
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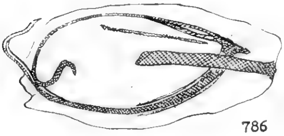
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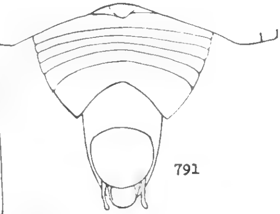
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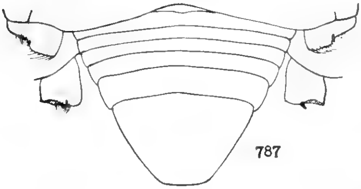
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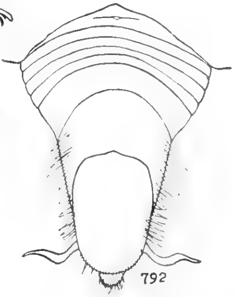
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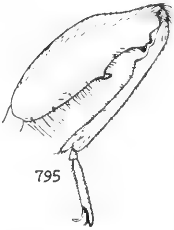
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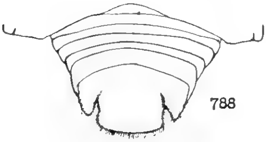
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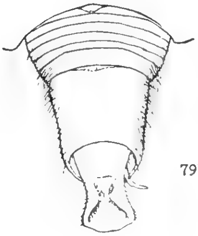
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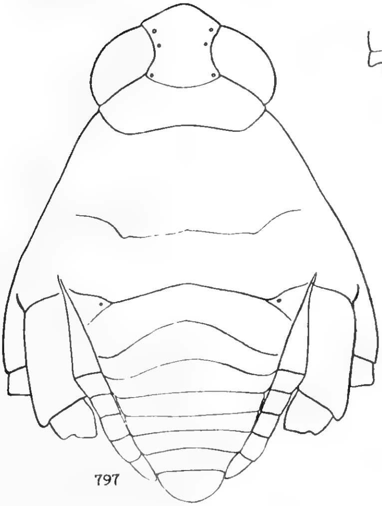
FIGURES 797-807

797. Dorsal view of male, *Eurymetra natalensis* (Distant).
798. Ventral view of female abdomen, *Eurymetra natalensis* (Distant).
799. Ventral view of male abdomen, *Eurymetra nitidulus* Esaki.
800. Ventral view of abdomen, *Eurymetra natalensis* (Distant).
801. Male front leg, *Eurymetra natalensis* (Distant).
802. Lateral view of head, *Eurymetra natalensis* (Distant).
803. Apical segment of endosoma, *Eurymetra natalensis* (Distant).
804. Front tarsus, *Eurymetra natalensis* (Distant).
805. Middle tarsus, *Eurymetra natalensis* (Distant).
806. Hind tarsus, *Eurymetra natalensis* (Distant).
807. Female genitalia, *Eurymetra natalensis* (Distant).

FIGURES 797-807



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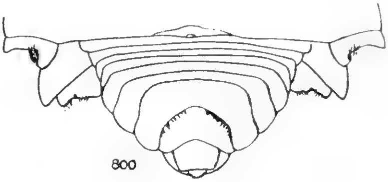

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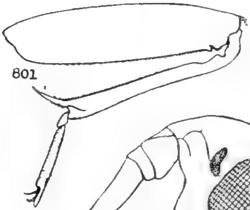

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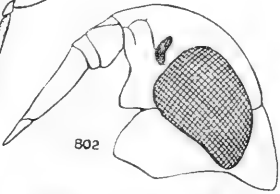

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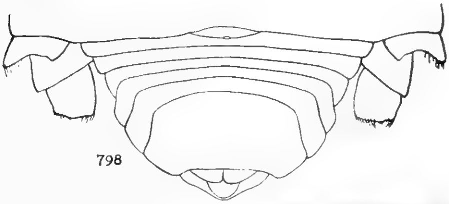

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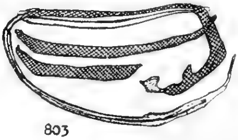

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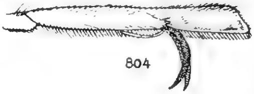

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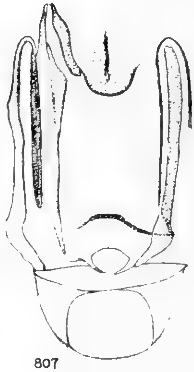

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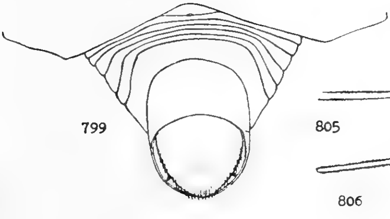

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FIGURES 808-818

808. Dorsal view of wingless female, *Eurymetropsiella schoutedeni* Poisson.

809. Lateral view of head in wingless female, *Eurymetropsiella schoutedeni* Poisson.

810. Female front leg, *Eurymetropsiella schoutedeni* Poisson.

811. Male front leg, *Eurymetropsiella schoutedeni* Poisson. Copied from Poisson (1950).

812. Female antenna, *Eurymetropsiella schoutedeni* Poisson.

813. Male antenna, *Eurymetropsiella schoutedeni* Poisson. Copied from Poisson (1950).

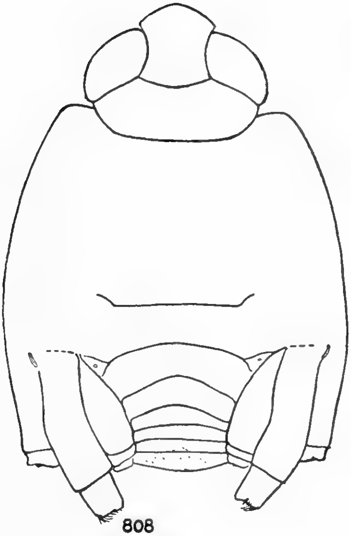
814. Ventral view of female abdomen, *Eurymetropsiella schoutedeni* Poisson.

815. Dorsal view of male genital segment, *Eurymetropsiella schoutedeni* Poisson. Copied from Poisson (1950).

816. Female hind coxa and trochanter, *Eurymetropsiella schoutedeni* Poisson.

818. Hind tarsus, *Eurymetropsiella schoutedeni* Poisson.

Figures 808-818



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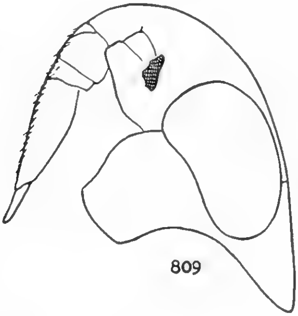

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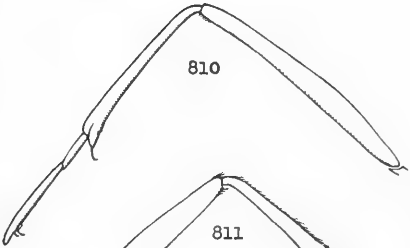

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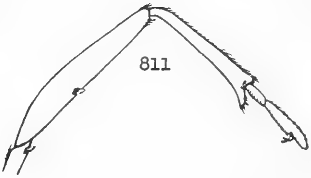

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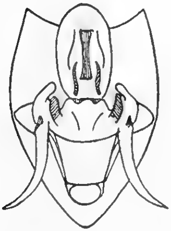

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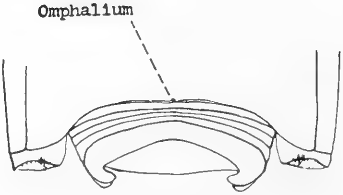

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FIGURES 819-825

819. Dorsal view of wingless female, *Ventidius (Ventidius) malayensis* Hungerford and Matsuda.

820. Dorsal view of winged female, *Ventidius (Ventidius) usingeri* Hungerford and Matsuda.

821. Forewing, *Ventidius (Ventidius) usingeri* Hungerford and Matsuda.

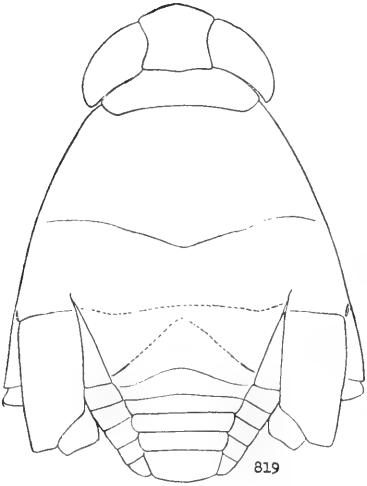
822. Lateral view of head, *Ventidius (Ventidius) malayensis* Hungerford and Matsuda.

823. Lateral view of head, *Ventidius (Ventidioides) kuiterti* Hungerford and Matsuda.

824. Ventral view of female, *Ventidius (Ventidius) usingeri* Hungerford and Matsuda.

825. Ventral view of male abdomen, *Ventidius (Ventidius) usingeri* Hungerford and Matsuda.

Figures 819-825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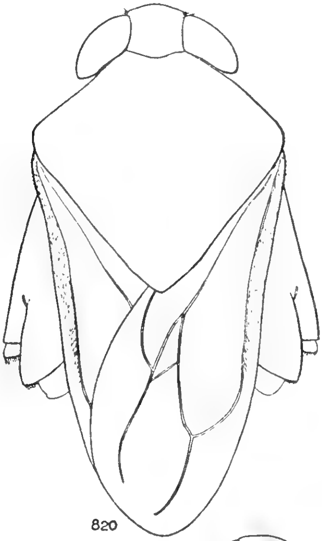
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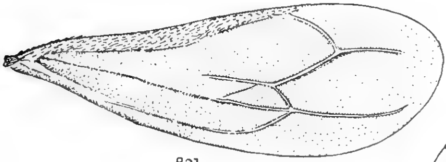
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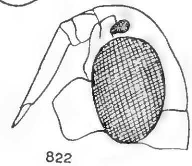
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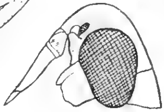
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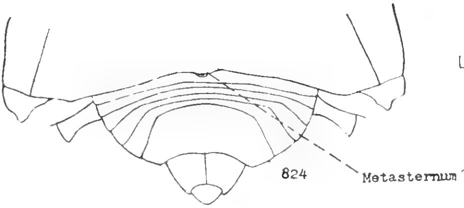
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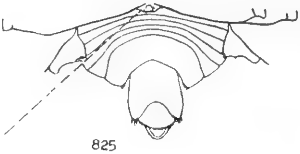
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FIGURES 826-838

826. Male antenna, *Ventidius (Ventidius) usingeri* Hungerford and Matsuda.

827. Male antenna, *Ventidius (Ventidius) malayensis* Hungerford and Matsuda.

828. Male antenna, *Ventidius (Ventidioides) kuiterti* Hungerford and Matsuda.

829. Ventral view of male abdomen, *Ventidius (Ventidius) malayensis* Hungerford and Matsuda.

830. Ventral view of male abdomen, *Ventidius (Ventidius) henryi* Esaki.

831. Ventral view of male abdomen, *Ventidius (Ventidioides) kuiterti* Hungerford and Matsuda.

832. Ventral view of female abdomen, *Ventidius (Ventidioides) kuiterti* Hungerford and Matsuda.

833. Lateral view of male genital segment, *Ventidius (Ventidius)* sp.

834. Apical segment of endosoma, *Ventidius (Ventidius) malayensis* Hungerford and Matsuda.

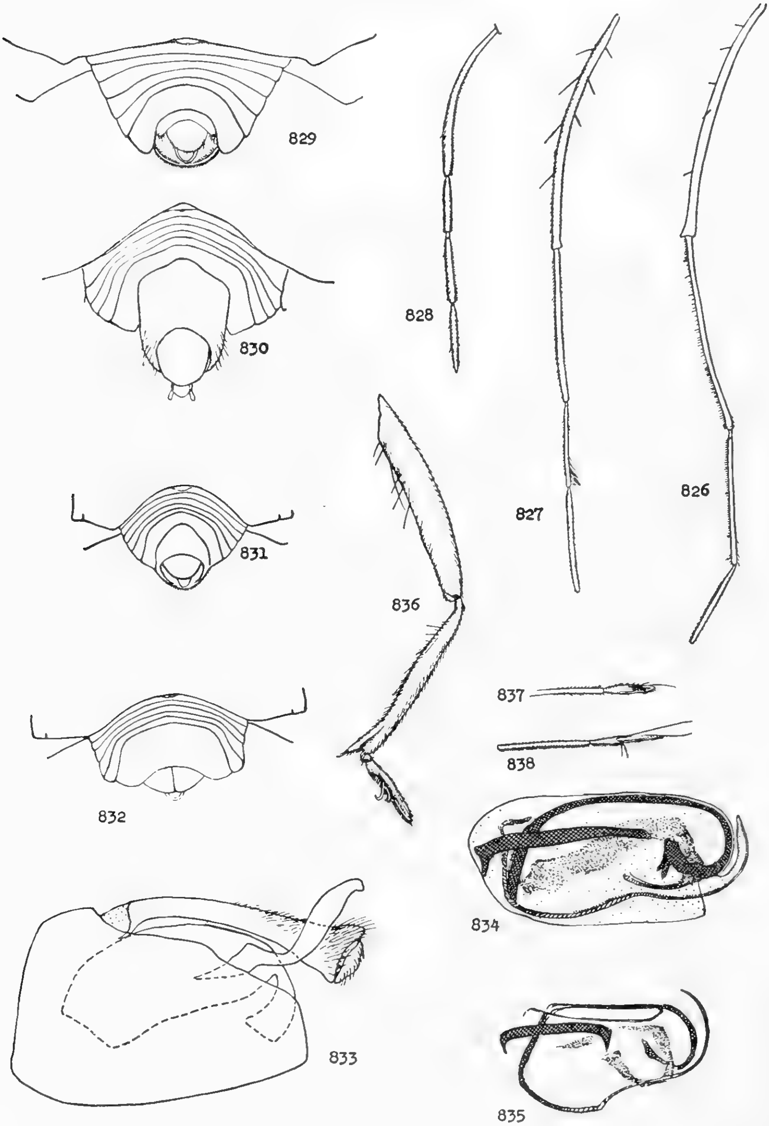
835. Apical segment of endosoma, *Ventidius (Ventidius) werneri* Hungerford and Matsuda.

836. Male front leg, *Ventidius (Ventidius) malayensis* Hungerford and Matsuda.

837. Middle tarsus, *Ventidius (Ventidius) malayensis* Hungerford and Matsuda.

838. Hind tarsus, *Ventidius (Ventidius) usingeri* Hungerford and Matsuda.

FIGURES 826-838



FIGURES 839-853

839. Dorsal view of winged male, *Ventidius (Ventidioides) kuiterti* Hungerford and Matsuda.

840. Ventral view of mesosternum, *Ventidius (Ventidioides) kuiterti* Hungerford and Matsuda.

841. Female genitalia, *Ventidius (Ventititioides) kuiterti* Hungerford and Matsuda.

842. Male front leg, *Ventidius (Ventidioides) kuiterti* Hungerford and Matsuda.

843. Apical segment of endosoma, *Ventidius (Ventidioides) kuiterti* Hungerford and Matsuda.

844. Lateral view of male genital segment, *Ventidius (Ventidioides) kuiterti* Hungerford and Matsuda.

845. Ventral view of male abdomen, *Eurymetropsielloides milloti* Poisson.

846. Ninth tergum, *Eurymetropsielloides milloti* Poisson. Copied from Poisson (1956).

847. Pygophore, *Eurymetropsielloides milloti* Poisson. Copied from Poisson (1956).

848. Paramere, *Eurymetropsielloides milloti* Poisson. Copied from Poisson (1956).

849. Front leg, *Eurymetropsielloides milloti* Poisson. Copied from Poisson (1956).

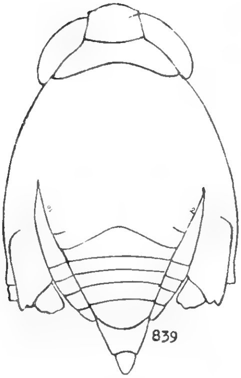
850. Hind leg, *Eurymetropsielloides milloti* Poisson. Copied from Poisson (1956).

851. Middle leg, *Eurymetropsielloides milloti* Poisson. Copied from Poisson (1956).

852. Male antenna, *Eurymetropsielloides milloti* Poisson. Copied from Poisson (1956).

853. Middle tarsus, *Eurymetropsielloides milloti* Poisson. Copied from Poisson (1956).

FIGURES 839-853



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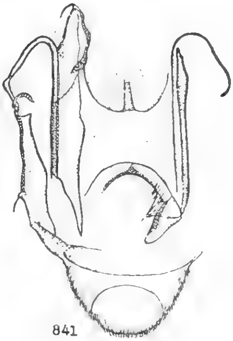

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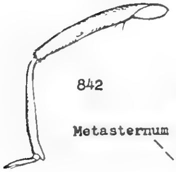

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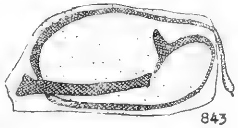

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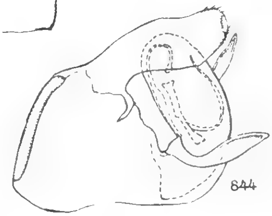

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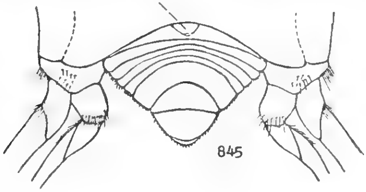

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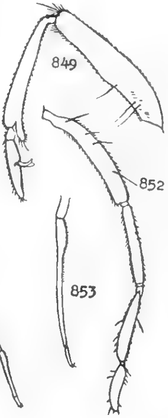

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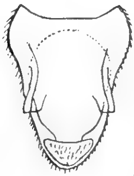

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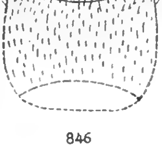

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FIGURES 854-863

854. Dorsal view of wingless male, *Esakia usingeri* Hungerford and Matsuda.

855. Winged male, *Esakia usingeri* Hungerford and Matsuda.

856. Nymph, *Esakia usingeri* Hungerford and Matsuda.

857. Ventral view of head, *Esakia usingeri* Hungerford and Matsuda.

858. Lateral view of head, *Esakia kuiterti* Hungerford and Matsuda.

859. Ventral view of female abdomen, *Esakia kuiterti* Hungerford and Matsuda.

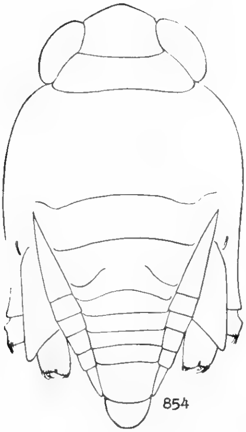
860. Ventral view of female apical abdominal segments, *Esakia kuiterti* Hungerford and Matsuda.

861. Male antenna, *Esakia usingeri* Hungerford and Matsuda.

862. Female antenna, *Esakia usingeri* Hungerford and Matsuda.

863. Female genitalia, *Esakia usingeri* Hungerford and Matsuda.

Figures 854-863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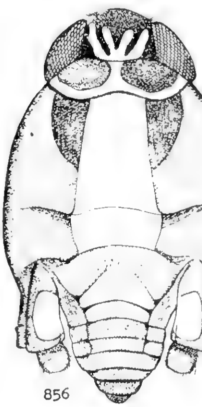
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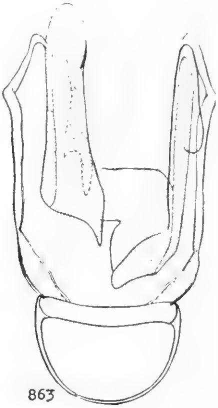
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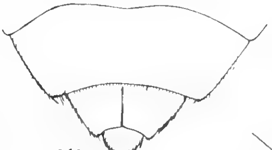
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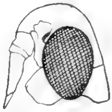
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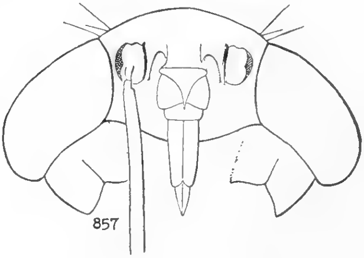
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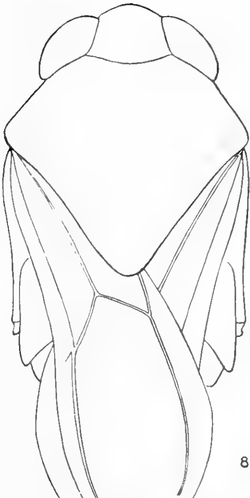
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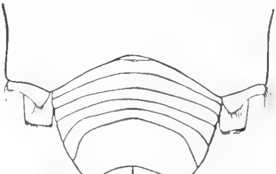
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FIGURES 864-880

864. Lateral view of thorax, *Esakia usingeri* Hungerford and Matsuda.

865. Ventral view of apical abdominal segments, *Esakia usingeri* Hungerford and Matsuda.

866. Lateral view of male genital segment, *Esakia usingeri* Hungerford and Matsuda.

867. Male front leg, *Esakia usingeri* Hungerford and Matsuda.

868. Middle leg, *Esakia kuiterti* Hungerford and Matsuda.

869. Middle tarsus, *Esakia usingeri* Hungerford and Matsuda.

870. Apical segment of endosoma, *Esakia kuiterti* Hungerford and Matsuda.

871. Hind tarsus, *Esakia kuiterti* Hungerford and Matsuda.

872. Dorsal view of wingless male, *Eurymetropsis carayoni* Poisson.

873. Lateral view of head, *Eurymetropsis carayoni* Poisson.

874. Female antenna, *Eurymetropsis carayoni* Poisson.

875. Front femur, *Eurymetropsis carayoni* Poisson. Copied from Poisson (1948).

876. Apex of tibia and base of tarsus in front leg, *Eurymetropsis carayoni* Poisson. Copied from Poisson (1948).

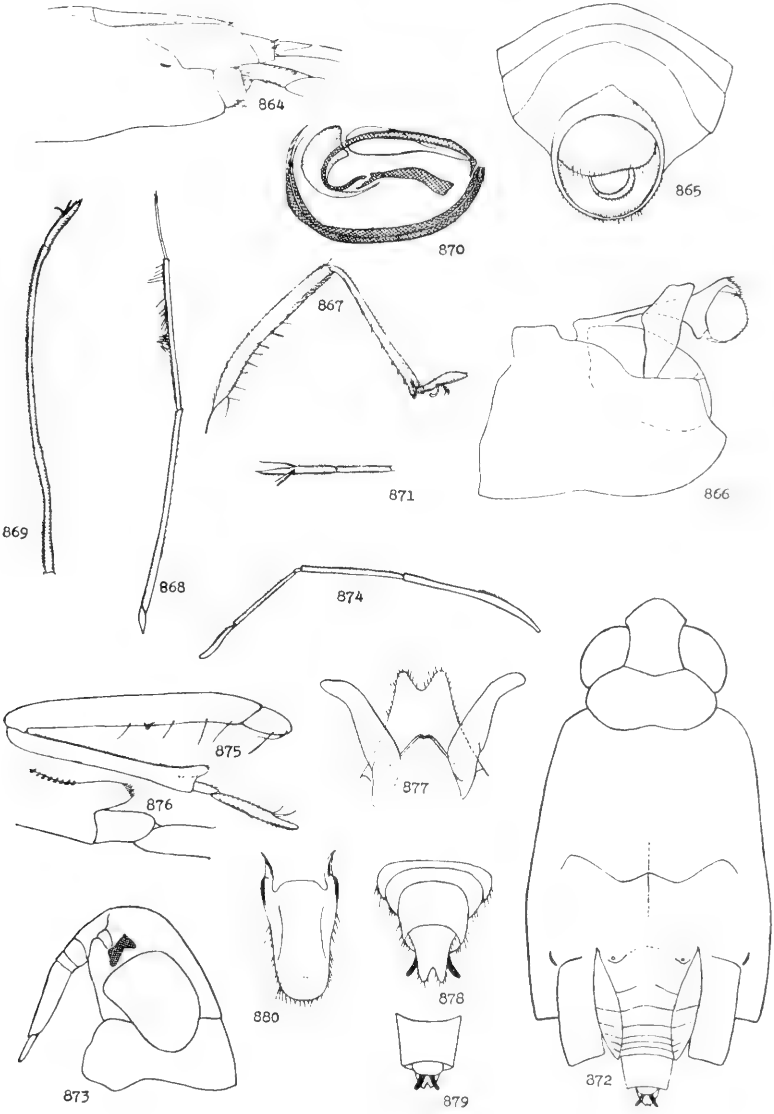
877. Paramere, *Eurymetropsis carayoni* Poisson. Copied from Poisson (1948).

878. Ventral view of male apical abdominal segments, *Eurymetropsis carayoni* Poisson. Copied from Poisson (1948).

879. Dorsal view of male apical abdominal segments, *Eurymetropsis carayoni* Poisson. Copied from Poisson (1948).

880. Suranal plate, *Eurymetropsis carayoni* Poisson. Copied from Poisson (1948).

FIGURES 864-880



FIGURES 881-891

881. Dorsal view of wingless male, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

882. Ventral view of metathorax and abdomen in male, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

883. Lateral view of head, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

884. Ventral view of female apical abdominal segments, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

885. Pronotum in winged form, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

886. Forewing, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

887. Hind wing, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

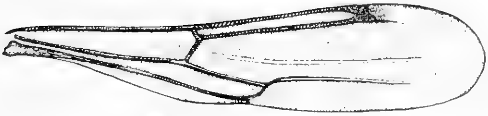
888. Female antenna, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

889. Male front leg, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

890. Lateral view of male genital segment, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

891. Apical segment of endosoma, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

Figures 881-891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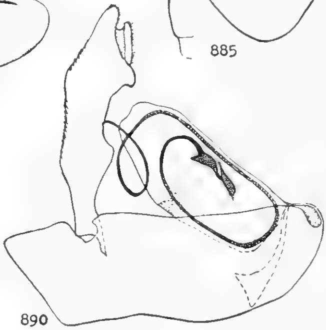
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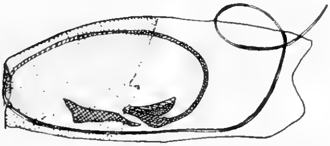
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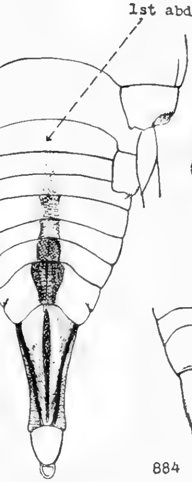
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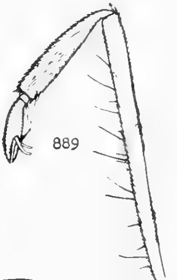
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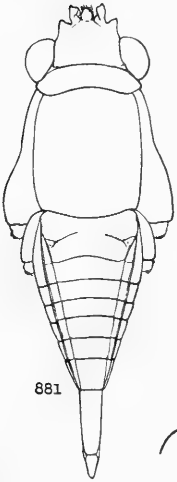
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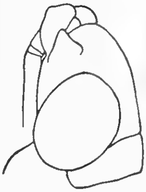
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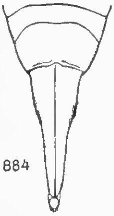
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FIGURES 892-903

892. Dorsal view of female, *Rhagadotarsus (Caprivia) hutchinsoni* China.

893. Ventral view of female metathorax and abdomen, *Rhagadotarsus (Caprivia) hutchinsoni* China.

894. Ventral view of female apical abdominal segments, *Rhagadotarsus (Caprivia) hutchinsoni* China.

895. Lateral view of head, *Rhagadotarsus (Caprivia) hutchinsoni* China.

896. Ventral view of head, *Rhagadotarsus (Caprivia) hutchinsoni* China.

897. Female genitalia, *Rhagadotarsus (Caprivia) hutchinsoni* China.

898. Female antenna, *Rhagadotarsus (Caprivia) hutchinsoni* China.

899. Female front leg, *Rhagadotarsus (Caprivia) hutchinsoni* China.

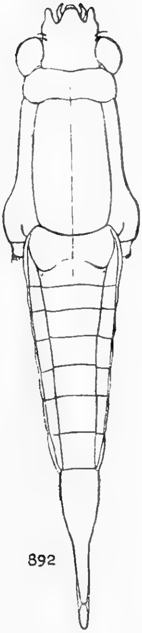
900. Middle last tarsal segment, *Rhagadotarsus (Caprivia) hutchinsoni* China.

901. Hind tarsus, *Rhagadotarsus (Caprivia) hutchinsoni* China.

902. Middle tarsus, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

903. Hind tarsus, *Rhagadotarsus (Rhagadotarsus) kraepelini* Breddin.

FIGURES 892-903



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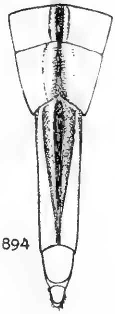

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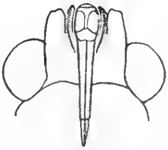

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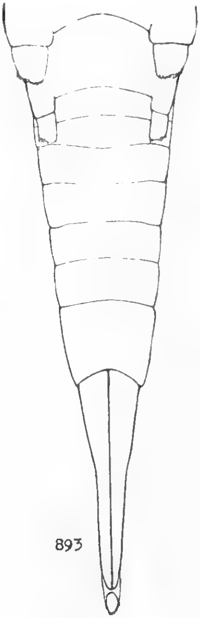

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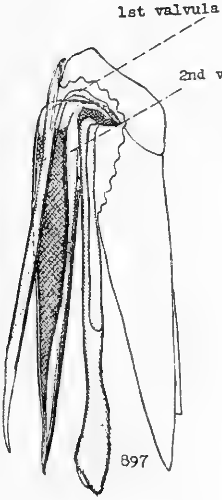

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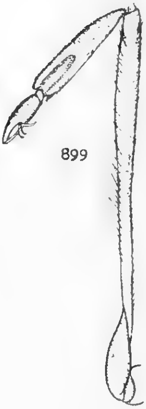

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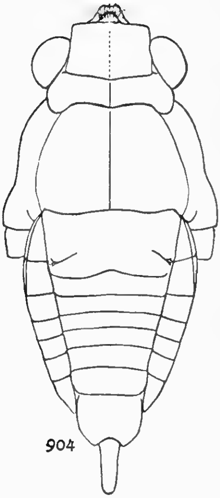
FIGURES 904-920

904. Dorsal view of wingless female, *Rheumatobates rileyi* Bergroth.
905. Lateral view of head, *Rheumatobates rileyi* Bergroth.
906. Forewing, *Rheumatobates crassifemur* Esaki.
907. Hind wing, *Rheumatobates crassifemur* Esaki.
908. Lateral view of male genital segment, *Rheumatobates crassifemur* Esaki.
909. Apical segment of endosoma, *Rheumatobates crassifemur* Esaki.
910. Ventral view of female abdominal segments, *Rheumatobates crassifemur* Esaki.
911. Female genitalia, *Rheumatobates crassifemur* Esaki.
912. Middle last tarsal segment, *Rheumatobates rileyi* Bergroth.
913. Hind tarsal segment, *Rheumatobates tenuipes* Meinert.
914. Male antenna, *Rheumatobates clanis* Drake and Harris.
915. Same, *Rheumatobates mangrovensis* (China).
916. Same, *Rheumatobates trinitatis* (China).
917. Same, *Rheumatobates bonariensis* (Berg).
918. Same, *Rheumatobates drakei* Hungerford.
919. Same, *Rheumatobates klagei* Schroeder.
920. Same, *Rheumatobates crassifemur* Esaki.

Figures 904-920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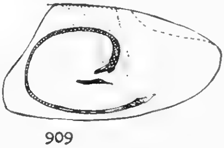
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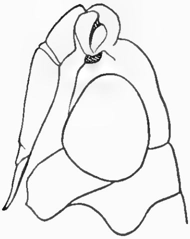
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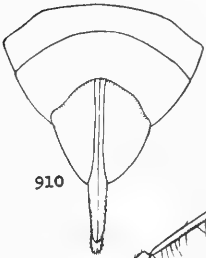
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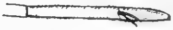
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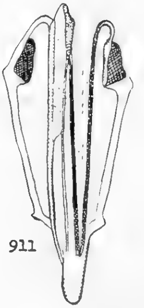
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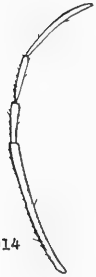
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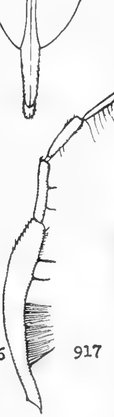
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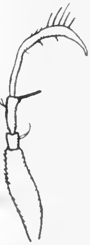
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FIGURES 921-938

921. Male antenna, *Rheumatobates citatus* Drake and Hottes.
922. Same, *Rheumatobates imitator* (Uhler).
923. Same, *Rheumatobates mexicanus* Drake and Hottes.
924. Same, *Rheumatobates bergrothi* Meinert.
925. Same, *Rheumatobates rileyi* Bergroth.
926. Same, *Rheumatobates tenuipes* Meinert.
927. Same, *Rheumatobates trulliger* Bergroth.
928. Same, *Rheumatobates hungerfordi* Wiley.
929. Female antenna, *Rheumatobates mangrovensis* (China).
930. Same, *Rheumatobates creaseri* Hungerford.
931. Same, *Rheumatobates clanis* Drake and Harris.
932. Same, *Rheumatobates vegatus* Drake and Harris.
933. Same, *Rheumatobates minutus* Hungerford.
934. Male antenna, *Rheumatobates petilus* Drake and Hottes.
935. Male front leg, *Rheumatobates minutus* Hungerford.
936. Same, *Rheumatobates vegatus* Drake and Harris.
937. Same, *Rheumatobates clanis* Drake and Harris.
938. Same, *Rheumatobates mangrovensis* (China).

Figures 921-938

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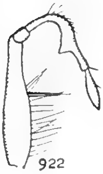

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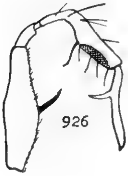

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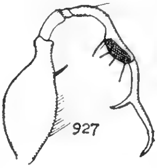

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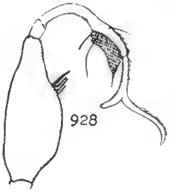

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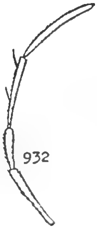

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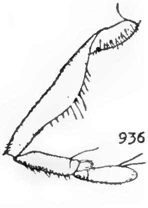

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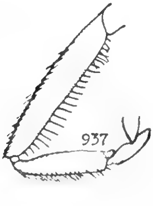

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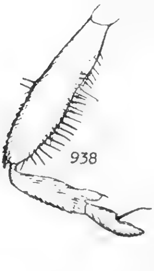

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FIGURES 939-949

939. Male front leg, *Rheumatobates klagei* Schroeder.
940. Same, *Rheumatobates citatus* Drake and Harris.
941. Same, *Rheumatobates trinitatis* (China).
942. Female front leg, *Rheumatobates petilus* Drake and Hottes.
943. Same, *Rheumatobates creaseri* Hungerford.
944. Same, *Rheumatobates crassifemur* Esaki.
945. Male middle leg, *Rheumatobates crassifemur* Esaki.
946. Same, *Rheumatobates klagei* Schroeder.
947. Same, *Rheumatobates rileyi* Bergroth.
948. Same, *Rheumatobates praeposterus* Bergroth.
949. Ventral view of male abdomen, *Rheumatobates citatus* Drake and Hottes.

FIGURES 939-949

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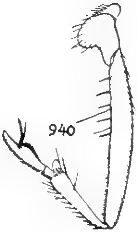

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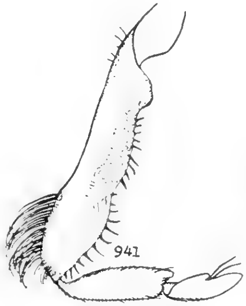

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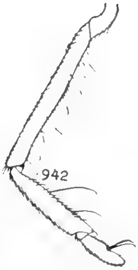

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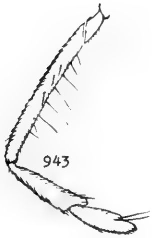

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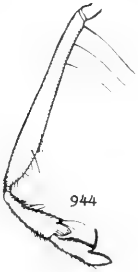

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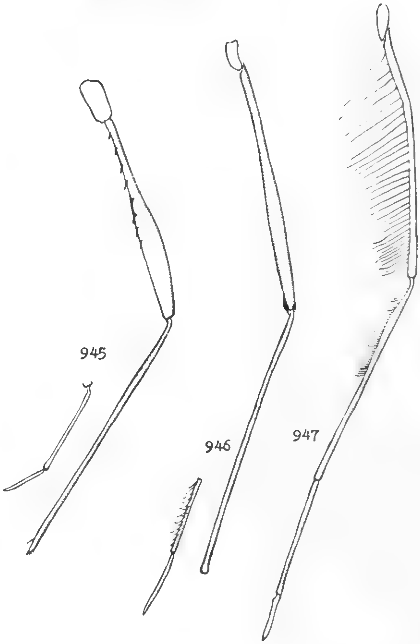

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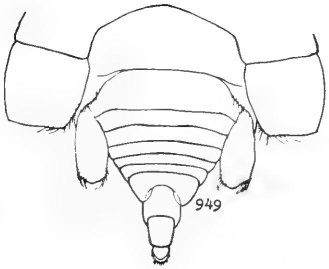

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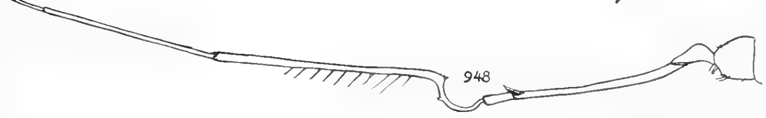

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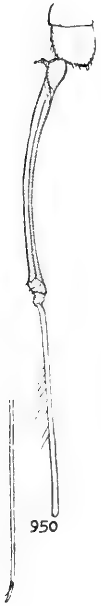
FIGURES 950-961

950. Male middle leg, *Rheumatobates citatus* Drake and Harris.
951. Male hind leg, *Rheumatobates tenuipes* Bergroth.
952. Same, *Rheumatobates citatus* Drake and Harris.
953. Same, *Rheumatobates hungerfordi* Wiley.
954. Same, *Rheumatobates trulliger* Bergroth.
955. Same, *Rheumatobates spinosus* Hungerford.
956. Same, *Rheumatobates crassifemur* Esaki.
957. Same, *Rheumatobates imitator* (Uhler).
958. Same, *Rheumatobates klagei* Schroeder.
959. Same, *Rheumatobates mexicanus* Drake and Hottes.
960. Same, *Rheumatobates rileyi* Bergroth.
961. Same, *Rheumatobates bergrothi* Meinert.

FIGURES 950-961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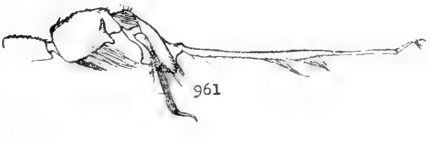
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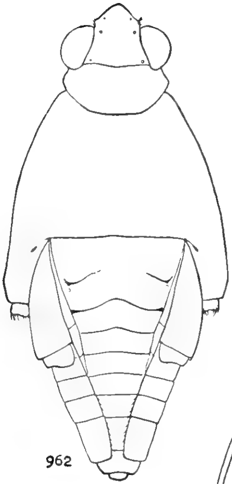
FIGURES 962-969

962. Dorsal view of wingless male, *Trepobates inermis* Esaki.
963. Ventral view of head, *Trepobates inermis* Esaki.
964. Pronotum in winged form, *Trepobates inermis* Esaki.
965. Ventral view of male abdomen, *Trepobates pictus* (Herrich-Schaeffer).
966. Antenna, *Trepobates inermis* Esaki.
967. Male front leg, *Trepobates pictus* (Herrich-Schaeffer).
968. Forewing, *Trepobates* sp.
969. Hind wing, *Trepobates* sp.

FIGURES 962-969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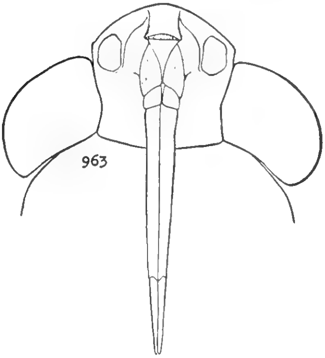
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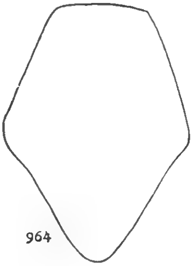
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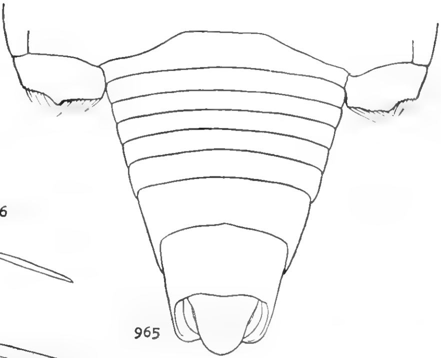
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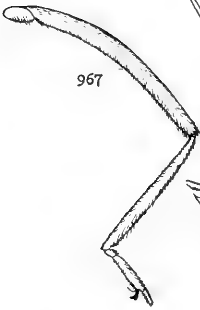
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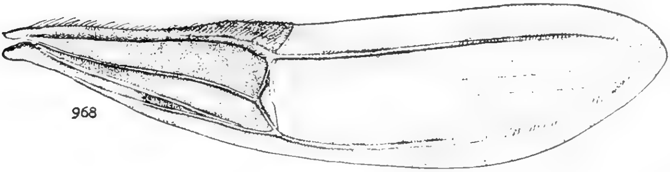
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FIGURES 970-980

970. Male femur, *Trepobates pictus* (Herrich-Schaeffer).

971. Middle last tarsal segment, *Trepobates pictus* (Herrich-Schaeffer).

972. Hind tarsus, *Trepobates pictus* (Herrich-Schaeffer).

973. Ventral view of female apical abdominal segments, *Trepobates inermis* Esaki.

974. Ventral view of female apical abdominal segments, *Trepobates pictus* (Herrich-Schaeffer).

975. Lateral view of female apical abdominal segments, *Trepobates* sp.

976. Female genitalia, *Trepobates knighti* Drake and Harris. First valvula folded cephalad.

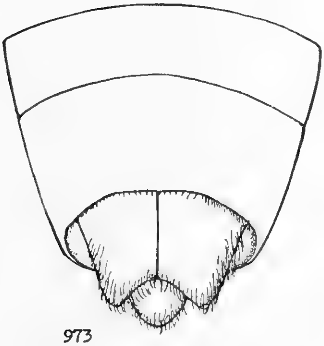
977. Lateral view of male genital segment, *Trepobates knighti* Drake and Harris.

978. Apical segment of endosoma, *Trepobates knighti* Drake and Harris.

979. Same, *Trepobates trepidus* Drake and Harris.

980. Lateral view of head, *Trepobates pictus* (Herrich-Schaeffer).

FIGURES 970-980



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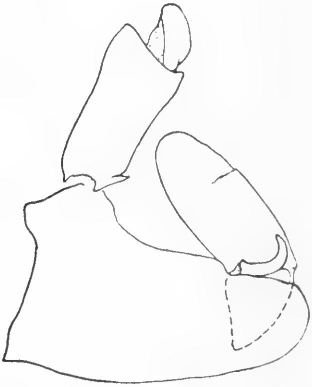

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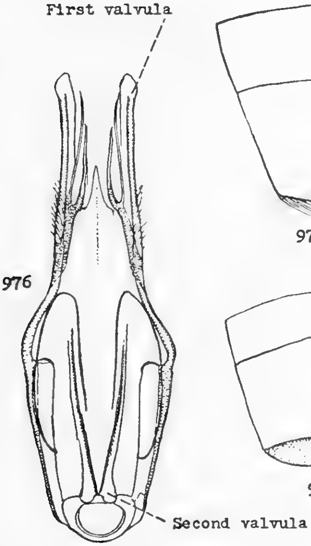

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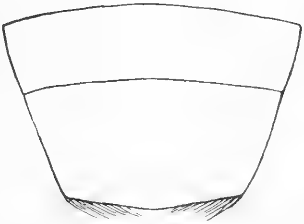

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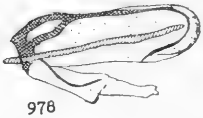

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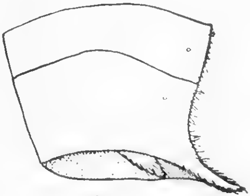

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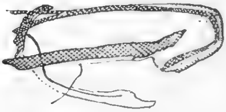

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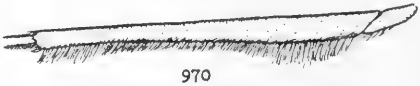

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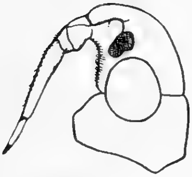

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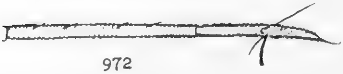

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FIGURES 981-991

981. Dorsal view of wingless female, *Telmatometra indentata* Kenaga.

982. Ventral view of wingless male, *Telmatometra ujhelji* Esaki.

983. Lateral view of head, *Telmatometra whitei* Bergroth.

984. Forewing, *Telmatometra whitei* Bergroth.

985. Hind wing, *Telmatometra whitei* Bergroth.

986. Lateral view of male genital segment, *Telmatometra whitei* Bergroth.

987. Female genitalia, *Telmatometra whitei* Bergroth. First valvula folded cephalad.

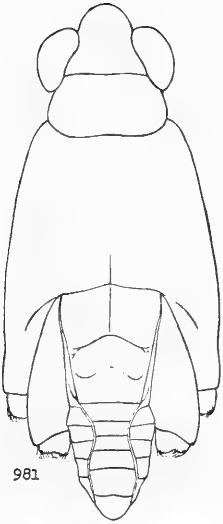
988. Apical segment of endosoma, *Telmatometra fusca* Kenaga.

989. Same, *Telmatometra whitei* Bergroth.

990. Same, *Telmatometra indentata* Kenaga.

991. Ventral view of male apical abdominal segments, *Telmatometra retusa* Kenaga.

FIGURES 981-991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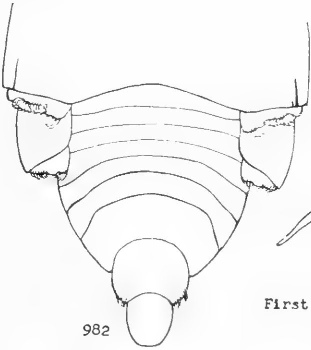
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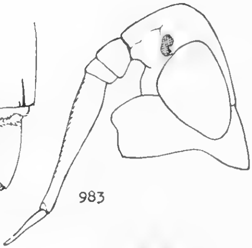
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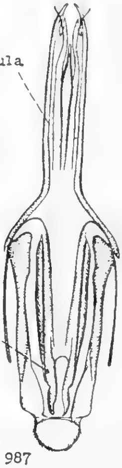

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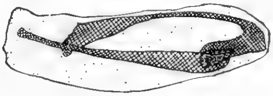
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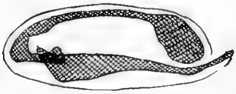
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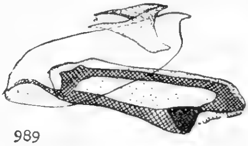
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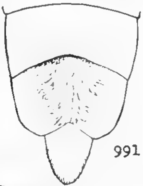
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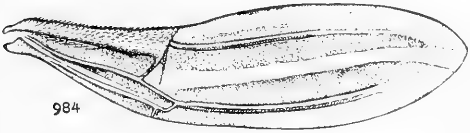
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986

FIGURES 992-1002

992. Dorsal view of wingless female, *Trepobatoides boliviensis* Hungerford and Matsuda.

993. Lateral view of head, *Trepobatoides boliviensis* Hungerford and Matsuda.

994. Ventral view of female abdomen, *Trepobatoides boliviensis* Hungerford and Matsuda.

995. Ventral view of male abdomen, *Trepobatoides boliviensis* Hungerford and Matsuda.

996. Apical segment of endosoma, *Trepobatoides boliviensis* Hungerford and Matsuda.

997. Lateral view of male genital segment, *Trepobatoides boliviensis* Hungerford and Matsuda.

998. Female genitalia, *Trepobatoides boliviensis* Hungerford and Matsuda.

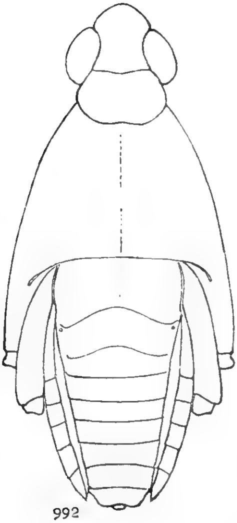
999. Male antenna, *Trepobatoides boliviensis* Hungerford and Matsuda.

1000. Female front leg, *Trepobatoides boliviensis* Hungerford and Matsuda.

1001. Hind tarsus, *Trepobatoides boliviensis* Hungerford and Matsuda.

1002. Middle tarsus, *Trepobatoides boliviensis* Hungerford and Matsuda.

Figures 992-1002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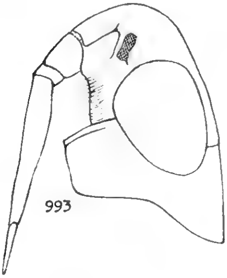
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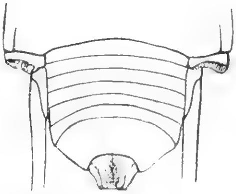
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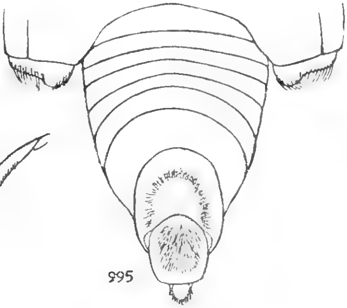
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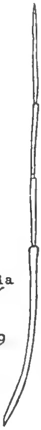
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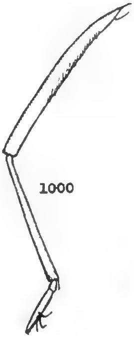
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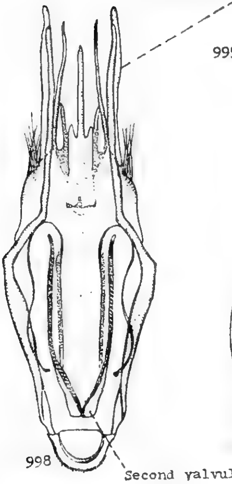
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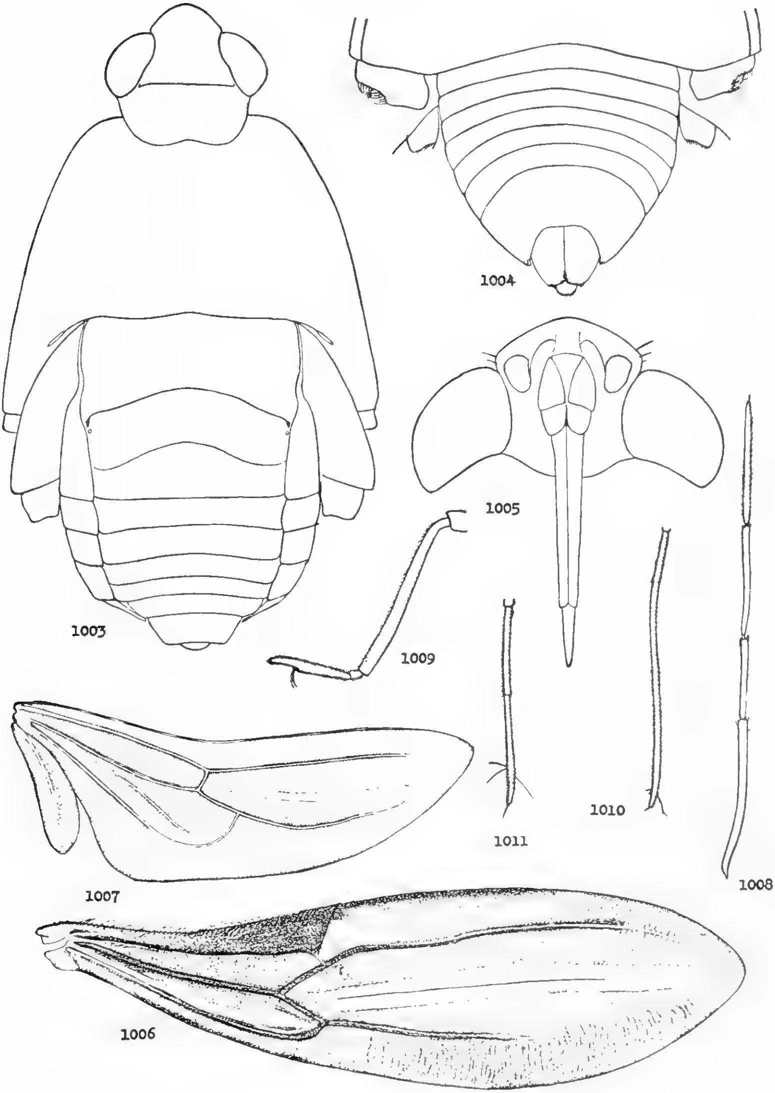
FIGURES 1003-1011

1003. Dorsal view of wingless female, *Halobatopsis platensis* (Berg).
1004. Ventral view of female abdomen, *Halobatopsis platensis* (Berg).
1005. Ventral view of head, *Halobatopsis platensis* (Berg).
1006. Forewing, *Halobatopsis spiniventris* Drake and Harris.
1007. Hind wing, *Halobatopsis spiniventris* Drake and Harris.
1008. Antenna, *Halobatopsis platensis* (Berg).
1009. Female tibia and tarsus, *Halobatopsis platensis* (Berg).
1010. Middle last tarsal segment, *Halobatopsis platensis* (Berg).
1011. Male hind tarsus, *Halobatopsis spiniventris* Drake and Harris.

Figures 1003-1011



FIGURES 1012-1025

1012. Ventral view of male apical abdominal segments, *Telmatometra acuta* Kenaga.

1013. Same, *Telmatometra indentata* Kenaga.

1014. Ventral view of female apical abdominal segments, *Telmatometra whitei* Bergroth.

1015. Female antenna, *Telmatometra whitei* Bergroth.

1016. Middle tarsus, *Telmatometra whitei* Bergroth.

1017. Female front leg, *Telmatometra whitei* Bergroth.

1018. Hind tarsus, *Telmatometra whitei* Bergroth.

1019. Lateral view of head, *Halobatopsis spiniventris* Drake and Harris.

1020. Dorsal view of wingless male, *Halobatopsis spiniventris* Drake and Harris.

1021. Ventral view of male apical abdominal segments, *Halobatopsis platensis* (Berg).

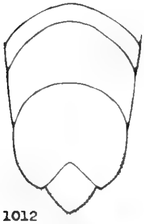
1022. Same, *Halobatopsis spiniventris* Drake and Harris.

1023. Lateral view of male genital segment, *Halobatopsis spiniventris* Drake and Harris.

1024. Apical segment of endosoma, *Halobatopsis platensis* Berg.

1025. Female genitalia, *Halobatopsis spiniventris* Drake and Harris. First valvulae are folded cephalad.

FIGURES 1012-1025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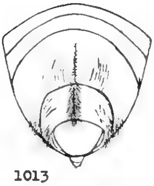
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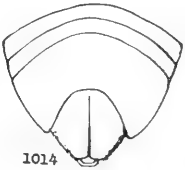
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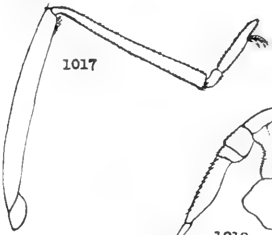
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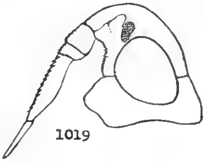
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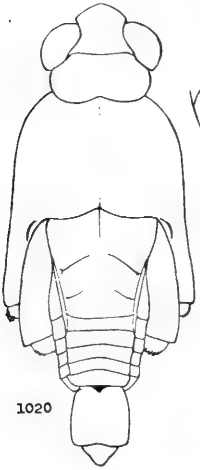
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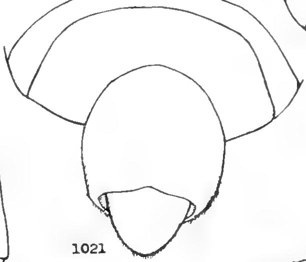
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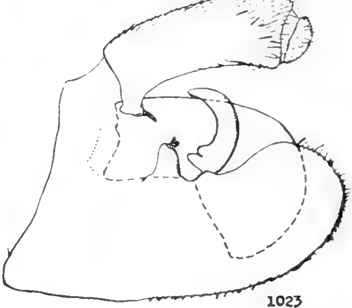
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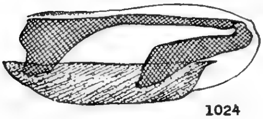
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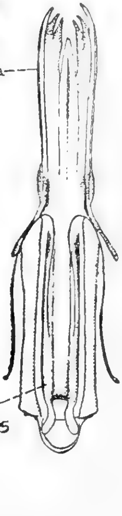

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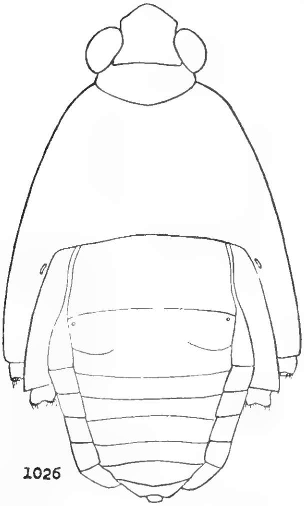
FIGURES 1026-1036

1026. Dorsal view of wingless female, *Ovatametra obesa* Kenaga.
1027. Ventral view of female abdomen, *Ovatametra obesa* Kenaga.
1028. Ventral view of head, *Ovatametra minima* Kenaga.
1029. Lateral view of head, *Ovatametra obesa* Kenaga.
1030. Ventral view of male apical abdominal segments, *Ovatametra obesa* Kenaga.
1031. Lateral view of male apical abdominal segments, *Ovatametra* sp.
1032. Apical segment of endosoma, *Ovatametra minima* Kenaga.
1033. Same, *Ovatametra* sp.
1034. Female antenna, *Ovatametra obesa* Kenaga.
1035. Female front tibia and tarsus, *Ovatametra obesa* Kenaga.
1036. Female genitalia, *Ovatametra fusca* Kenaga.

FIGURES 1026-1036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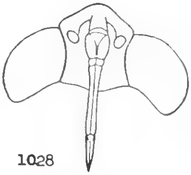
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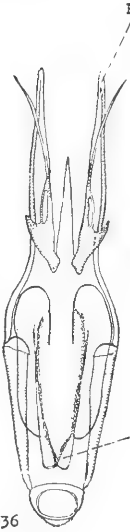

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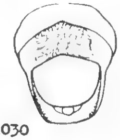
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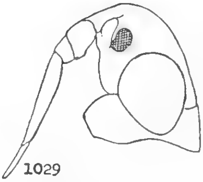
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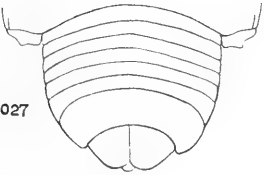
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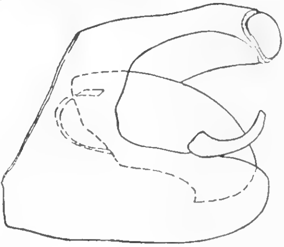
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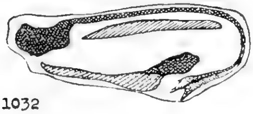
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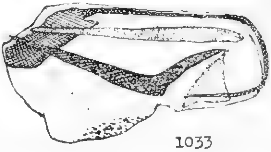
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FIGURES 1037-1047

1037. Dorsal view of wingless male, *Rheumatometroides browni* Hungerford and Matsuda.

1038. Dorsal view of wingless female, *Rheumatometroides browni* Hungerford and Matsuda.

1039. Lateral view of male apical abdominal segments, *Rheumatometroides browni* Hungerford and Matsuda.

1040. Lateral view of head, *Rheumatometroides browni* Hungerford and Matsuda.

1041. Apical segment of endosoma, *Rheumatometroides browni* Hungerford and Matsuda.

1042. Female front leg, *Rheumatometroides browni* Hungerford and Matsuda.

1043. Middle tarsus, *Rheumatometroides browni* Hungerford and Matsuda.

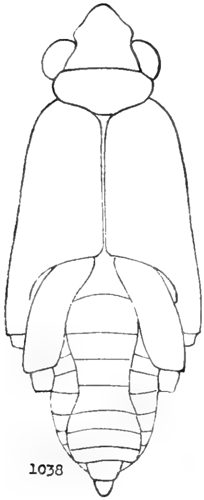
1044. Hind tarsus, *Rheumatometroides browni* Hungerford and Matsuda.

1045. Female genitalia, *Rheumatometroides browni* Hungerford and Matsuda. First valvulae folded cephalad.

1046. Female antenna, *Rheumatometroides browni* Hungerford and Matsuda.

1047. Ventral view of female abdomen, *Rheumatometroides browni* Hungerford and Matsuda.

FIGURES 1037-1047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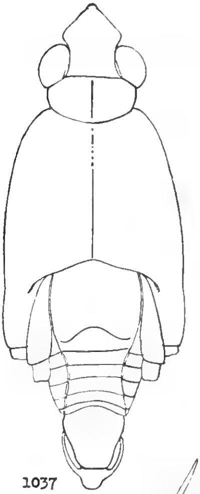
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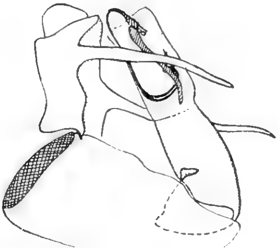
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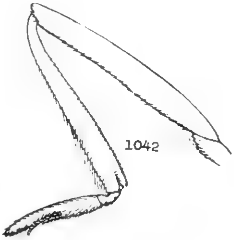
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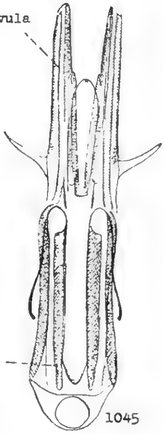
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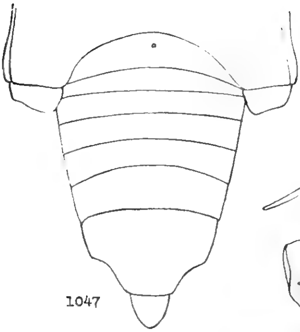
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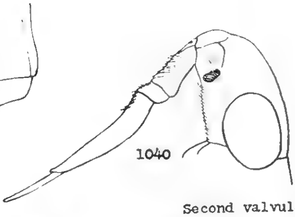
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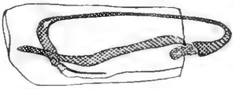
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FIGURES 1048-1057

1048. Ventral view of female abdomen, *Rheumatometroides browni* Hungerford and Matsuda.

1049. Ventral view of male abdomen, *Rheumatometroides browni* Hungerford and Matsuda.

1050. Dorsal view of wingless male, *Stenobates biroi* (Esaki).

1051. Lateral view of head, *Stenobates biroi* (Esaki).

1052. Ventral view of male abdomen, *Stenobates biroi* (Easki).

1053. Lateral view of male apical abdominal segments, *Stenobates biroi* (Esaki).

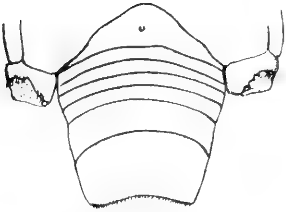
1054. Antenna, *Stenobates biroi* (Esaki).

1055. Male front leg, *Stenobates biroi* (Esaki).

1056. Hind tibia and tarsus, *Stenobates biroi* (Eskai).

1057. Middle tarsus, *Stenobates biroi* (Esaki).

Figures 1048-1057



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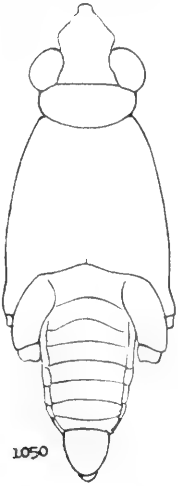

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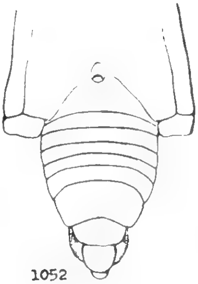

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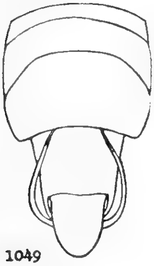

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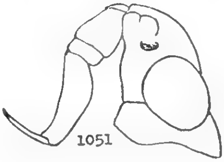

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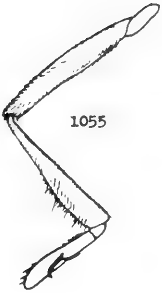

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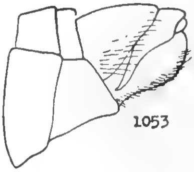

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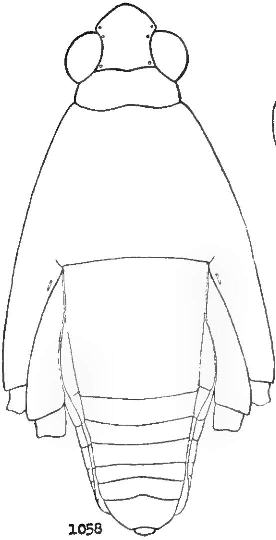
FIGURES 1058-1067

1058. Dorsal view of wingless female, *Cryptobates raja* (Distant).
1059. Ventral view of head, *Cryptobates raja* (Distant).
1060. Lateral view of head, *Cryptobates raja* (Distant).
1061. Pronotum in winged form, *Cryptobates raja* (Distant).
1062. Forewing, *Cryptobates raja* (Distant).
1063. Ventral view of female abdomen, *Cryptobates raja* (Distant).
1064. Antenna, *Cryptobates raja* (Distant).
1065. Front leg, *Cryptobates raja* (Distant).
1066. Middle tarsus, *Cryptobates raja* (Distant).
1067. Hind tarsus, *Cryptobates raja* (Distant).

Figures 1058-1067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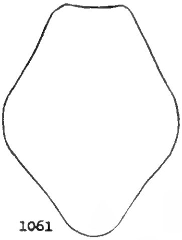
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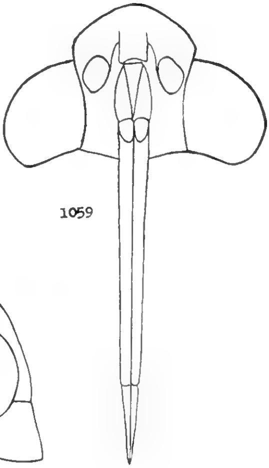
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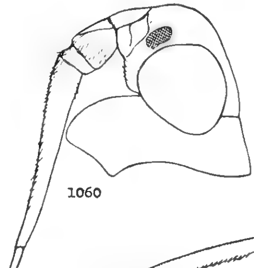
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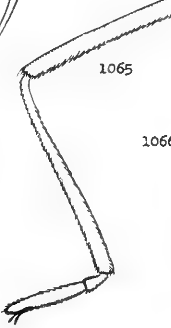
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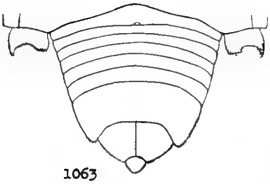
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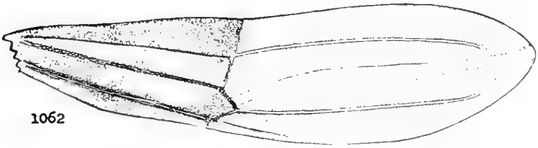
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FIGURES 1068-1080

1068. Lateral view of male genital segment, *Cryptobates raja* (Distant). (Distant).

1069. Apical segment of endosoma, *Cryptobates raja* (Distant).

1070. Same, *Cryptobates kuiterti* Hungerford and Matsuda.

1071. Female genitalia, *Cryptobates kuiterti* Hungerford and Matsuda. First valvulae folded cephalad.

1072. Dorsal view of wingless female, *Naboandelus bergevini* Bergroth.

1073. Dorsal view of winged female, *Naboandelus signatus* Distant.

1074. Lateral view of head, *Naboandelus bergevini* Bergroth.

1075. Ventral view of head, *Naboandelus signatus* Distant.

1076. Ventral view of female abdomen, *Naboandelus signatus* Distant.

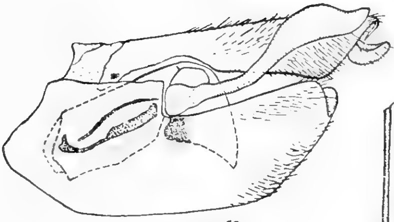
1077. Female front leg, *Naboandelus bergevini* Bergroth.

1078. Middle tarsus, *Naboandelus bergevini* Bergroth.

1079. Hind tibia and tarsus, *Naboandelus bergevini* Bergroth.

1080. Female genitalia, *Naboandelus* sp. from Burma. First valvulae folded cephalad.

FIGURES 1068-1080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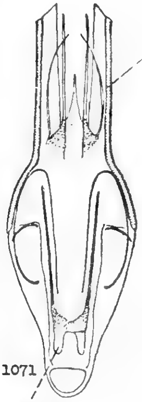

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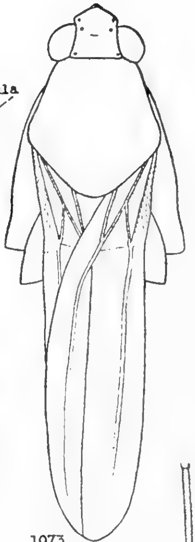
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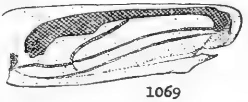
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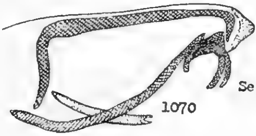
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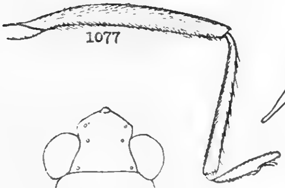
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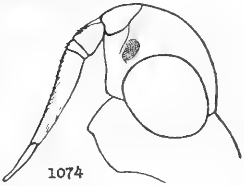
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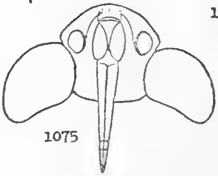
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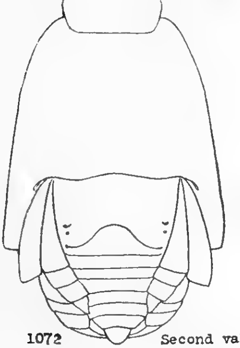
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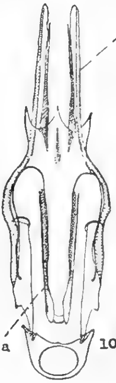

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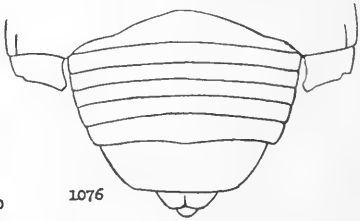
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FIGURES 1081-1092

1081. Dorsal view of wingless female, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1082. Ventral view of head, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1083. Lateral view of head, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1084. Ventral view of male abdomen, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1085. Ventral view of female abdomen, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1086. Surnal plate, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1087. Antenna, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1088. Male front leg, *Hynesionella omer-cooperi* Hungerford and Matsuda.

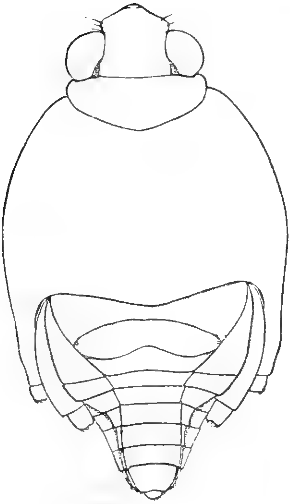
1089. Middle tarsus, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1090. Hind tarsus, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1091. Apical segment of endosoma, *Hynesionella omer-cooperi* Hungerford and Matsuda.

1092. Female genitalia, *Hynesionella omer-cooperi* Hungerford and Matsuda. First valvulae folded cephalad.

Figures 1081-1092



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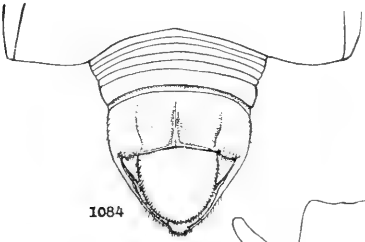

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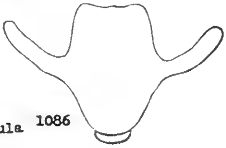

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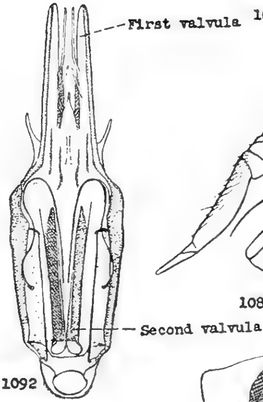

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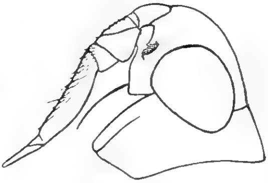

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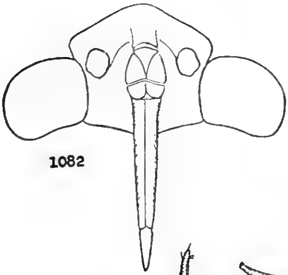

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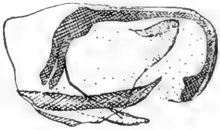

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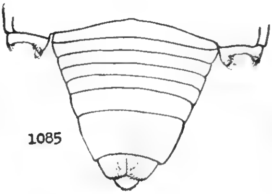

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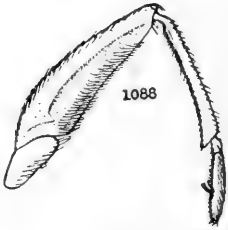

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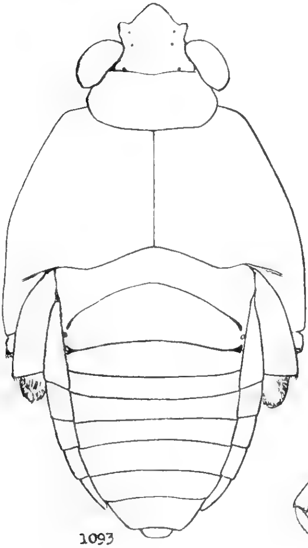
FIGURES 1093-1099

1093. Dorsal view of wingless female, *Metrobates denticornis* (Champion).
1094. Ventral view of head, *Metrobates denticornis* (Champion).
1095. Lateral view of head, *Metrobates tumidus* Anderson.
1096. Ventral view of male abdomen, *Metrobates denticornis* (Champion).
1097. Ventral view of mesosternum, *Metrobates porcus* Anderson.
1098. Forewing, *Metrobates denticornis* (Champion).
1099. Male front leg, *Metrobates denticornis* (Champion).

FIGURES 1093-1099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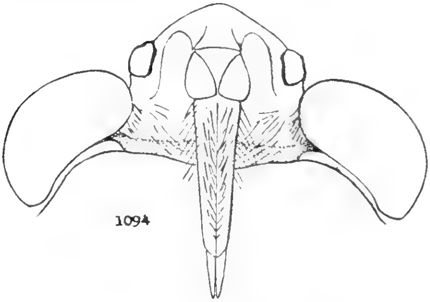
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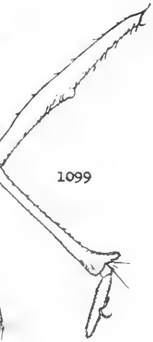
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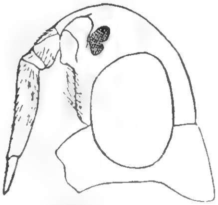
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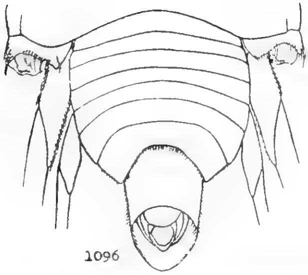
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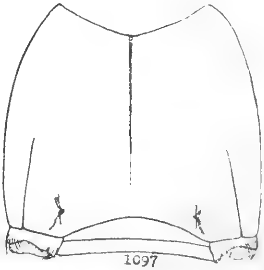
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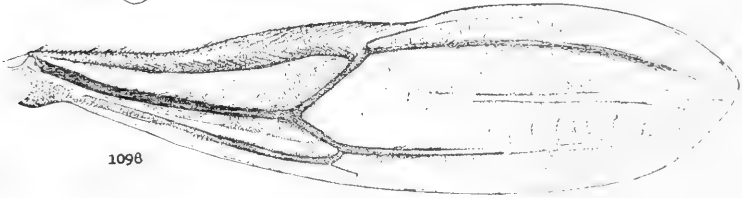
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FIGURES 1100-1108

1100. Hind wing, *Metrobates denticornis* (Champion).

1101. Nymph, *Metrobates porcus* Anderson.

1102. Ventral view of male apical abdominal segments, *Metrobates plaumanni* Hungerford.

1103. Lateral view of male apical abdominal segments, *Metrobates hesperius* Uhler.

1104. Apical segment of endosoma, *Metrobates hesperius* Uhler.

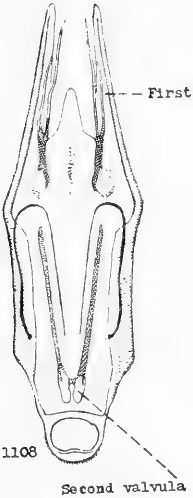
1105. Antenna, *Metrobates denticornis* (Champion).

1106. Middle tarsus, *Metrobates plaumanni* Hungerford.

1107. Hind tarsus, *Metrobates denticornis* (Champion).

1108. Female genitalia, *Metrobates hesperius* Uhler. First valvulae folded cephalad.

FIGURES 1100-1108



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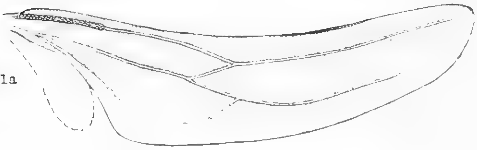

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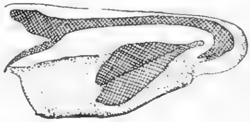

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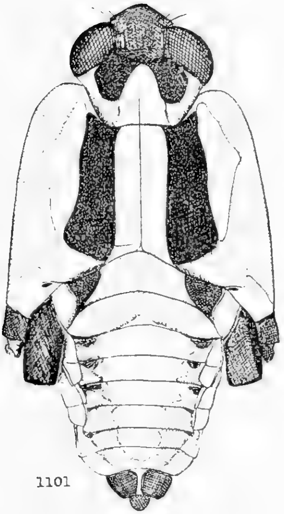

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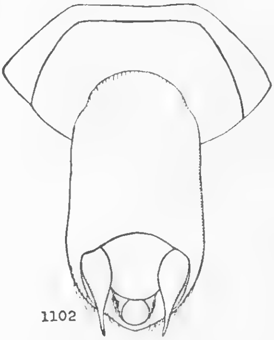

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FIGURES 1110-1121

1110. Dorsal view of wingless male, *Rheumatometra philarete* Kirkaldy.

1111. Ventral view of male abdomen, *Rheumatometra philarete* Kirkaldy.

1112. Ventral view of female abdomen, *Rheumatometra philarete* Kirkaldy.

1113. Lateral view of mesothorax, *Rheumatometra philarete* Kirkaldy.

1114. Lateral view of head, *Rheumatometra philarete* Kirkaldy.

1115. Forewing, *Rheumatometra philarete* Kirkaldy.

1116. Hind wing, *Rheumatometra philarete* Kirkaldy.

1117. Lateral view of male apical abdominal segments, *Rheumatometra philarete* Kirkaldy.

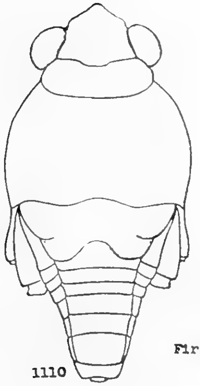
1118. Apical segment of endosoma, *Rheumatometra philarete* Kirkaldy.

1119. Middle tarsus, *Rheumatometra philarete* Kirkaldy.

1120. Hind tarsus, *Rheumatometra philarete* Kirkaldy.

1121. Female genitalia, *Rheumatometra philarete* Kirkaldy. First valvulae folded cephalad.

Figures 1110-1121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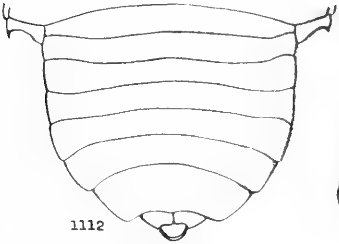
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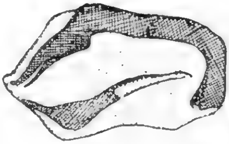
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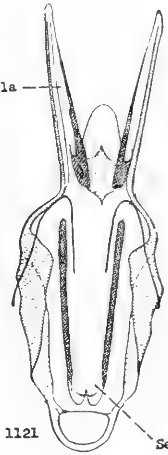

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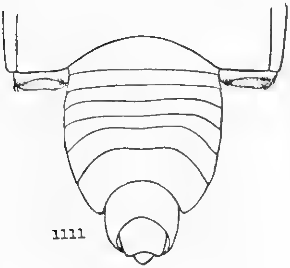
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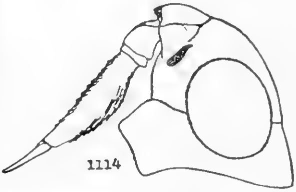
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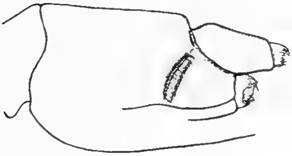
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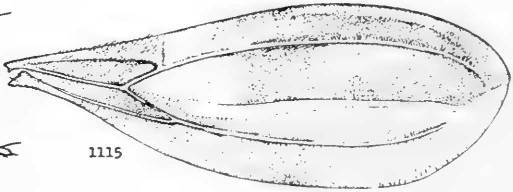
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FIGURES 1122-1134

1122. Dorsal view of wingless female, *Metrobatopsis flavonotus* Esaki.

1123. Ventral view of head, *Metrobatopsis flavonotus* Esaki.

1124. Lateral view of head, *Metrobatopsis* sp.

1125. Forewing, *Metrobatopsis flavonotus* Esaki.

1126. Ventral view of male abdomen, *Metrobatopsis flavonotus* Esaki.

1127. Lateral view of male apical abdominal segments, *Metrobatopsis solomonensis* Hungerford and Matsuda.

1128. Lateral view of apical segment of endosoma, *Metrobatopsis flavonotus* Esaki.

1129. Dorsal view of apical segment of endosoma, *Metrobatopsis flavonotus* Esaki.

1130. Pronotum in winged form, *Metrobatopsis flavonotus* Esaki.

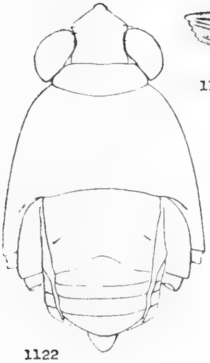
1131. Male antenna, *Metrobatopsis solomonensis* Hungerford and Matsuda.

1132. Female antenna, *Metrobatopsis flavonotus* Esaki.

1133. Male front leg, *Metrobatopsis solomonensis* Hungerford and Matsuda.

1134. Female genitalia, *Metrobatopsis flavonotus* Esaki. First valvulae folded cephalad.

Figures 1122-1134



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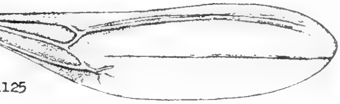

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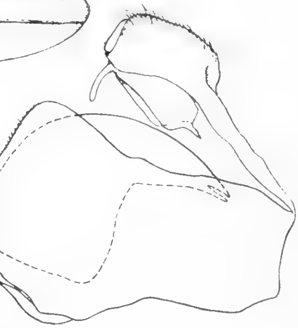

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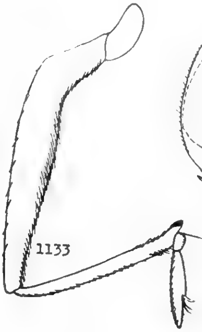

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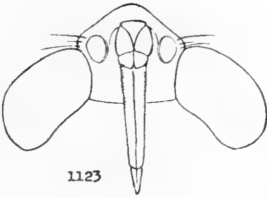

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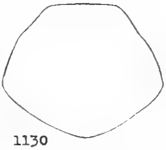

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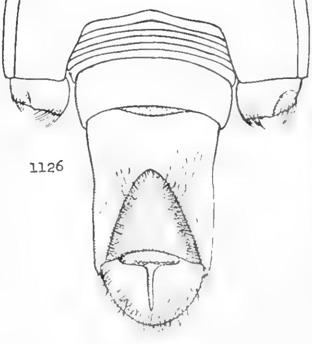

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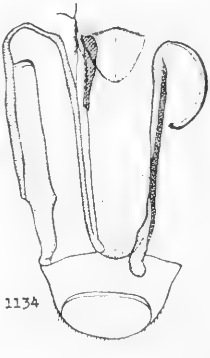

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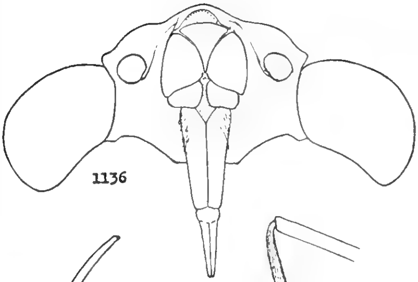
FIGURES 1135-1144

1135. Dorsal view of wingless female, *Rheumatometra philarete* Kirkaldy.
1136. Ventral view of head, *Rheumatometra philarete* Kirkaldy.
1137. Female middle femur, *Rheumatometra philarete* Kirkaldy.
1138. Ventral view of female abdomen, *Metrobatopsis* sp. from New Guinea.
1139. Female antenna, *Rheumatometra philarete* Kirkaldy.
1140. Female front leg, *Rheumatometra philarete* Kirkaldy.
1141. Male front leg, *Rheumatometra philarete* Kirkaldy.
1142. Ventral view of male abdomen, *Metrobatopsis affinis* Esaki.
1143. Dorsal view of female abdomen, *Metrobatopsis* sp. from the Solomon Islands.
1144. Dorsal view of female abdomen, *Metrobatopsis* sp. from the Solomon Islands.

FIGURES 1135-1144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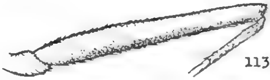
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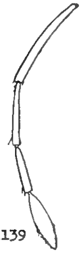
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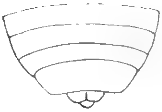
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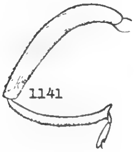
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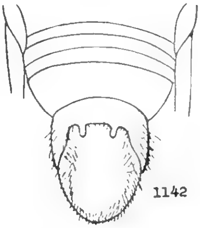
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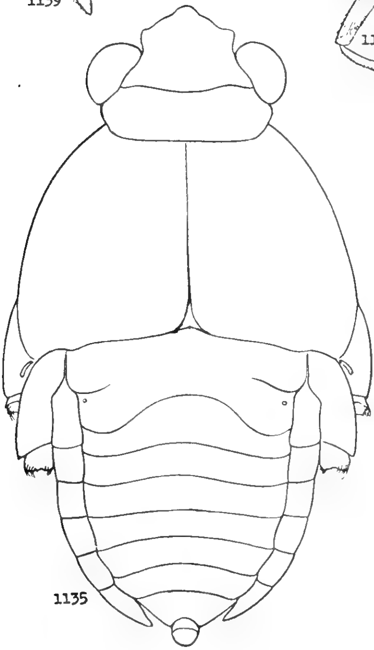
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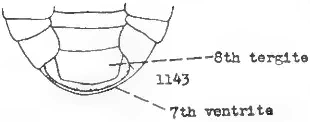
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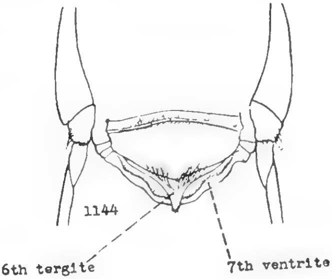
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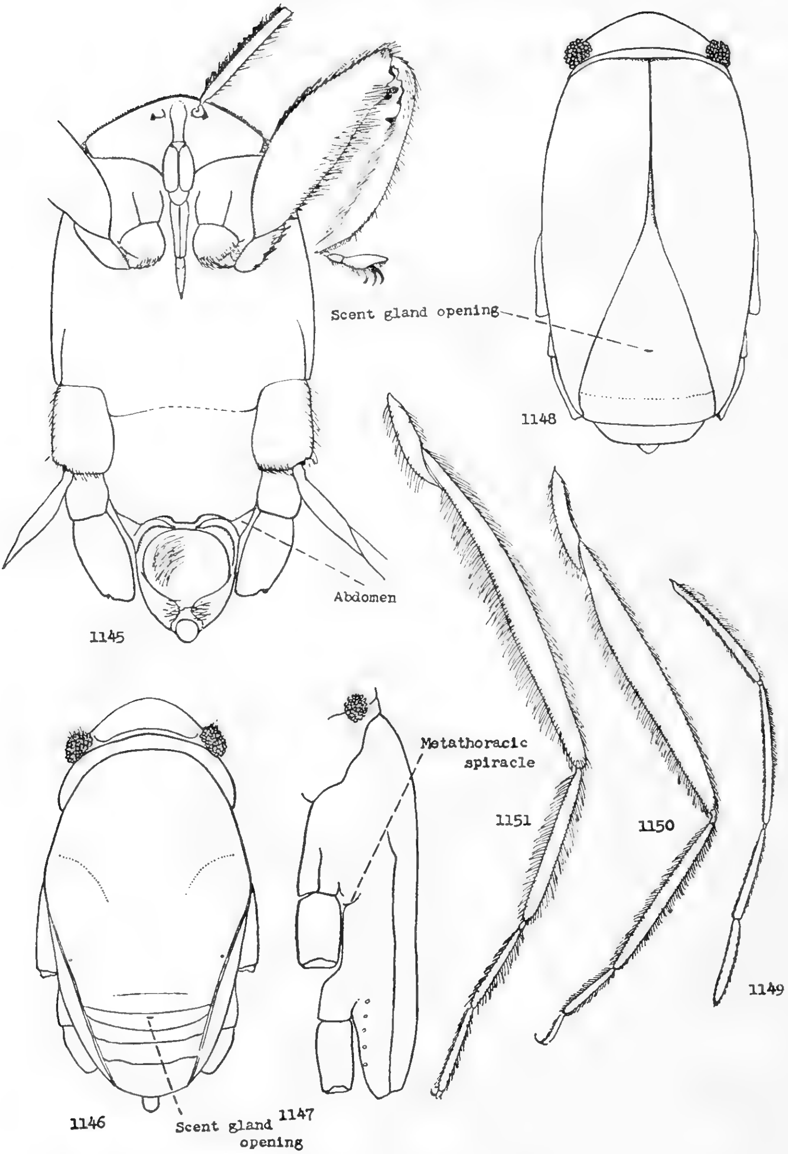
Figures 1145-1151



1145. Ventral view of male, *Hermatobates weddi* China.
1146. Dorsal view of male, *Hermatobates weddi* China.
1147. Lateral view of male, *Hermatobates weddi* China.
1148. Dorsal view of female, *Hermatobates weddi* China.
1149. Antenna, *Hermatobates weddi* China.
1150. Male middle leg, *Hermatobates weddi* China.
1151. Male hind leg, *Hermatobates weddi* China.

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Serological and Chemical Studies on Gamma-Irradiated Ovalbumin

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INTRODUCTION

One of the most characteristic properties of proteins is their capacity to undergo denaturation. Denaturation refers to physical or intramolecular rearrangement rather than to chemical alteration of the native molecule. Denaturation of proteins can be investigated in terms of alteration of physicochemical properties or in terms of loss of biological activity as compared to the native molecule. A standard criterion for the denaturation of protein is the loss of solubility at the isoelectric point of the native molecule.

Fricke (1952a, 1952b) has demonstrated that ionizing radiations cause a denaturation of proteins, as defined by a loss of solubility at the isoelectric point. He has shown that, in addition to the molecules that are insoluble at the isoelectric point, irradiated ovalbumin contains other structurally altered molecules that can be identified by their increased thermal lability and subsequent loss of solubility at the isoelectric point. Fricke, Leone, and Landmann (1957) have reported that it has not yet been determined to what extent radiation-denaturation is correlated with loss of biological activity. In order to make some correlation between denaturation and loss of biological activity due to irradiation, experiments were designed to measure these properties in ovalbumin. Specifically, the extent of degradation, the increase in thermal lability, and the loss of serological activity of gamma-irradiated, lyophilized ovalbumin were studied.

MATERIALS AND METHODS

Native ovalbumin

All ovalbumin samples were obtained from the Worthington Biochemical Company, Freehold, N. J. The manufacturer prepared the ovalbumin by recrystallizing it two times with sodium sulfate (Kekwick and Cannan, 1936.) The ovalbumin was then lyophilized. After being received in this laboratory it was stored at —20° C. until used.

Irradiation

Samples of ovalbumin to be irradiated were warmed to room temperature and placed in ampules that were then evacuated to $10\text{-}15 \times 10^{-3}$ mm. Hg. Vacuum-sealed ampules were placed in Dewar flasks, packed with ice, and irradiated in a homogeneous field of gamma rays at a rate of 1.5×10^{6} rad/hour in the High Gamma Facility at Argonne National Laboratory, Lemont, Ill. The radiation dosages were determined by means of the Fricke-Hart dosimeter (Hart and Walsh, 1954). Radiation was expressed in terms of electron volts absorbed per molecule (ev/m) where 1 ev/m is equivalent to 0.217×10^{6} rads. All irradiated samples were stored at —20° C. until they were studied.

Solvation of protein

Native and irradiated ovalbumins were dissolved in water at 5° C. and maintained between pH 7.0 and 9.0 with 0.1 N NaOH in order to minimize any alteration of the protein molecule due to pH and temperature effects. Small amounts of ovalbumin were added to the water at intervals, with care, in order to maintain the pH within this range. As the protein was dissolved, the pH of the solution decreased. When the solution approached pH 7.0, the 0.1 N NaOH was added to raise the pH to approximately 9.0. After maximum solvation was obtained, the pH of the solution was adjusted to 7.2.

Fricke, Leone, and Landmann (1957) have indicated that the pH must be carefully controlled during the process of solvation in as much as instability of irradiated ovalbumin is induced at pH 9.2, and instability of native ovalbumin is induced at pH 12.0. Solutions of ovalbumin, in common with many protein systems, maintain the greatest degree of stability at 0° C. Once dissolved, all solutions of ovalbumin were kept at 0-5° C. Freezing the solutions was avoided because it induced the formation of measurable amounts of insoluble components when they were subsequently melted.

Protein determinations

In the process of irradiation small fragments containing nitrogen are split off the native protein. The protein-nitrogen accordingly decreases in concentration with increasing dosages of irradiation. However, Fricke, Leone, and Landmann (1957) have found that at dosages below 100 ev/m the loss of nitrogen does not significantly alter the concentration of protein-nitrogen as determined by the Kjeldahl method. Two modifications of the Kjeldahl procedure were used in the determination of nitrogen.

In the first series of determinations of nitrogen, the standard micro-Kjeldahl procedure was used (Kabat and Mayer, 1948). Ovalbumin was digested in concentrated sulfuric acid plus copper sulfate and a few crystals of potassium sulfate. Following digestion the material was steam-distilled. The distillate was collected in two percent boric acid and titrated with 0.1 N HC1 to determine the milliequivalents of nitrogen present. The factor of 6.5 was used in the conversion of protein-nitrogen to protein.

In the second series of nitrogen determination, the micro-Nessler procedure of Lanni, Dillon and Beard (1950) was used. Two tenths ml of a suitable dilution of ovalbumin was digested with 0.15 ml of 1:1.2 H_2SO_4 in 13 × 100 mm Pyrex test tubes. The organic material was oxidized by 30% H_2O_2. The digested material was diluted with water and treated with Nessler's reagent. The Beckman Model B Spectrophotometer was used for the measurement of the optical density of the nesslerized solution. Values obtained were readily converted to milliequivalents of nitrogen. All determinations were made in duplicate.

Preparation of antiserum

The antisera used in the serological tests were produced against native ovalbumin. Rabbits of 6 to 10 pounds were used for the production of antisera. Since ovalbumin by itself is a poor antigen, one percent solutions of ovalbumin were emulsified with equal parts of Difco Freund's Adjuvant. Injections of the emulsion were given subcutaneously on alternate days in the volumes: 0.5 ml, 1.0 ml, 2.0 ml, and 4.0 ml. Two days following this series of injections 8.0 ml of the emulsion was given intraperitoneally. After allowing 7 to 10 days for the production of antibodies in the rabbit, 50 ml of blood were removed by cardiac puncture. Several series of injections were administered to each rabbit. Each series was followed by a partial bleeding of 50 ml. After each sample of blood had completely clotted, the clear serum was separated and stored at —20° C.

Terminology

The solutions of native and irradiated ovalbumin were designated as N or I, respectively. In thermal fractionations of ovalbumin (Figures 1 and 2) the prefixes N or I were used to identify respectively each fraction obtained from native or irradiated preparations of protein. NS_1, for example, would identify the first supernatant fraction from native ovalbumin and IS_3 would identify the third supernatant fraction is a given sample of irradiated ovalbumin. D was the fraction of protein that was insoluble at pH 4.85, the isoelectric point of native ovalbumin. The thermolabile protein fraction that, after heating, was insoluble at pH 4.85 was designated as L. The supernatants obtained from the various precipitations were termed S. More specifically, S_1 was the supernatant which was soluble at pH 4.85 before the application of heat. Additional subscripts were used to designate the period of heating. Thus, S_{1-5} correspond to heating S_1 for a period of five hours.

S_2 was the protein solution that was soluble at pH 4.85 after S_1 had been heated at 50° C. for six hours. L_2 was the thermolabile fraction of S_1. S_3 was the protein solution which was soluble at pH 4.85 after S_2 was heated at 60° C. for six hours. L_2 was the thermolabile fraction obtained after S_2 was heated at 60° C. for six hours. S_4 was the protein which was soluble at pH 4.85 after S_3 was heated at 68° C. for two hours. L_3 was the fraction containing the thermolabile constituents obtained by heating S_3 for two hours at 68° C. and precipitating at the isoelectric point.

Thermal fractionations

The first group of experiments was devised to determine the effect of the pH of the solutions of protein during a thermal inactivation of protein (Figure 1). Freshly dissolved solutions of native and irradiated ovalbumin were allowed to stand overnight to permit maximum solvation. The solutions were adjusted at 0° to 3° C. to pH 4.85 with 0.1 N HC1 in order to precipitate any ovalbumin that was insoluble at its isoelectric point. After standing 18 hours in the refrigerator the supernatant solutions were cleared by centrifugation and each was divided into two portions. One portion was buffered at pH 4.85 with 0.1 M acetic acid and 0.1 M sodium acetate. The other portion was adjusted to pH 7.2 with 0.1 M NaOH and buffered at this pH with 0.06 M KH_2PO_4 and 0.06 M Na_2HPO. The isoelectrically insoluble protein (D) of the native and irradiated ovalbumins were washed three times with cold water at pH 4.85 and dissolved in cold water maintained between pH 7.0 and 9.0 with 0.1 N NaOH. The solutions of D were then adjusted to pH 7.2.

Aliquots of the supernatants (S_1), at both the acidic and the neutral pH, were measured into test tubes and heated at 50° C. ± 0.1° C. for intervals of one hour, five hours, and ten hours. Other aliquots of the same S_1 fraction at the neutral pH were heated for one hour, two hours, four hours, six hours, and ten hours at 60° C. ± 0.1° C. for any one experiment. After the specified time of heating, the tubes containing S_1 were plunged into ice water to prevent further heat-effects. The samples buffered to pH 7.2 during the heating process were adjusted to pH 4.85 with 0.1 N HC1. The tubes were allowed to stand overnight to ensure complete precipitation of the isoelectrically insoluble protein. All of the tubes were centrifuged and the supernatants decanted. The concentrations of protein in the original solutions (N or I), the D fraction, the S_1 and the various heated supernatants were determined. Serological tests were then run on all fractions.

The second group of heat inactivation analyses and heat fractionations (Figure 2) were run on an unbuffered system at pH 7.2. D was precipitated immediately following solvation and centrifuged at five and fifteen minute intervals after precipitation. S_1 was divided into aliquots for heating at 50° C. for one hour, two hours, four hours, and six hours. After each period of heating the denatured protein was precipitated immediately by adjustment of the pH to the isoelectric point of native ovalbumin, pH 4.85. The supernatant obtained from the aliquot that was heated for six hours (S_2) was further divided into four aliquots and heated at 60° C. for one hour, two hours, four hours, and six hours, respectively. The denatured constituents formed at 60° C. immediately were precipitated by adjusting the pH to 4.85. An aliquot of the material heated for six hours (S_3) at 60° C. was incubated at 68° C. for two hours (S_4). After each heating period the denatured protein was removed by adjusting the pH to 4.85.

Serological testing

In all serological tests the precipitin reaction was obtained by mixing varying quantities of antigen with a constant amount of antibody. Three types of serological tests were used. The first type consisted of a doubling dilution sequence of the protein covering a range from 212 μgm protein/ml to 6.25 μgm protein/ml. In this range, precipitin reactions in the equivalence zone were obtained as well as reactions in the region of both antigen and antibody excess. All ovalbumin fractions were diluted with neutral, phosphate-buffered, physiological saline. The serological tests were incubated for eighteen to twenty-four hours at a temperature of 0° C. to 5° C. The turbidity formed by the antigen-antibody reactions was measured on the Libby Photronreflectometer (Libby, 1938). The reliability of this instrument in turbidimetric serological procedures has been substantiated by Bolton, Leone, and Boyden (1948).

Because only six doubling dilutions of protein were used in the serological tests, it was necessary to measure the region of maximum reaction more precisely. In the second type of turbidimetric precipitin test a ten percent dilution-sequence of the solution of ovalbumin was made to include the region of the equivalence zone and also the regions of slight antigen excess and slight antibody excess. A constant volume of antibody was added to the dilutions of the antigen.

The nesslerization procedure of Lanni and co-workers (1950) was used as the third method for measuring the precipitin reactions. The antigen was serially diluted by a factor of 1.2 to cover a range from 35 μgm N/tube to 2 μgm N/tube. The antiserum was diluted so that the peak of the precipitin curve occurred at 7 to 8 μgm N/tube with native ovalbumin when a constant volume of 0.2 ml of antiserum was added to 0.2 ml of the diluted antigen. The precipitin tests were incubated 72 hours at 0° C. to 5° C. The tubes containing the antigen-antibody mixtures were centrifuged and the precipitates then washed two times with saline. The precipitates were digested with sulfuric acid and after nesslerization the nitrogen content was measured colorimetrically in a Beckman Model B Spectrophotometer (McDuffie and Kabat, 1956).

EXPERIMENTAL RESULTS

Thermal fractionations

In the first experiments solutions of N and I were allowed to stand 18 hours at pH 4.85, the isoelectric point of native ovalbumin, before D was removed by centrifugation. It was found that an average of 2.0 percent of the lyophilized and dissolved native ovalbumin was insoluble at the isoelectric point. In the samples of protein that had absorbed 60 ev/m, an average of 45.0 percent of the original material was precipitated at the isoelectric point. In the samples that had absorbed 30 ev/m, an average of 32.0 percent of the original protein was removed from solution by adjustment of the pH to 4.85.

In an attempt to ascertain whether or not time was a critical factor in the removal of D from the solutions when they were at pH 4.85, the amount of protein precipitated was determined after five minutes and fifteen minutes at this pH. After five minutes 0.4 to 0.5 percent of the native protein solution was removed. After fifteen minutes approximately 2.0 percent of the native ovalbumin was removed. After standing five minutes the D fraction of the 15 ev/m sample comprised 5.2 percent of I. After standing fifteen minutes before centrifugation 11.5 percent of I was removed. In the sample which had absorbed 30 ev/m, 11.6 percent of I was removed by centrifugation when allowed to stand five minutes. After the sample was allowed to stand fifteen minutes 22.2 percent of I was insoluble at the isoelectric point. In the irradiated sample which had absorbed 60 ev/m, 14.8 percent of I was removed as D when allowed to stand five minutes. On standing eighteen to twenty-four hours, 40.0 to 45.0 percent of I was removed. Table I contains a summary of the study relating time to the yield of D.

The L fractions obtained following heatings at pH 7.2 were completely soluble in water pH 9.0. However, the L fractions obtained by heating at pH 4.85 were either insoluble or only slightly soluble in water at pH 9.0.

Heat denaturation curves for irradiated and native ovalbumin are illustrated in Figure 3. At either temperature the most rapid removal of thermolabile substances from native ovalbumin occurred during the first hour of heating. After two hours of heating little if any additional protein material was removed from the native ovalbumin. At 50° C. both the 30 ev/m and the 60 ev/m samples showed the most rapid removal of the thermolabile substances during the first hour of incubation. After two hours essentially all the labile components were removed.

At a temperature of 60° C. the samples which had absorbed 60 ev/m showed a much greater loss of protein initially than did the 30 ev/m. After heating for four hours, essentially all the thermolabile molecules at 60° C. were removed. A six-hour heating period was required to remove the thermolabile components at this temperature in the samples which had absorbed 30 ev/m. The native ovalbumin lost protein at an essentially constant rate up to four hours of heating. However, the total loss of protein did not exceed 11.0 percent of the original native solution.

Thermal inactivations of isoelectrically soluble components in native and irradiated systems of ovalbumin are shown in Figure 4.

Table II shows that the percent recovery of ovalbumin of the N or I, the S_1, and the S_2 fractions generally fell within the range of 95.0 to 100.0 percent. The percentage of ovalbumin recovered in the S_3 fraction was usually much lower. Whether this was due to the formation of nonprotein fragments of protein was not determined.

The percentage of ovalbumin, expressed in terms of the original N or I solutions, that remained in the various supernatants is given in Table III. In this series of experiments the following determinations were made: three fractionations of native ovalbumin; two fractionations of 15 ev/m samples; one fractionation of a 30 ev/m sample; and two fractionations of 60 ev/m samples. The variability shown in Table III is that obtained from replicate determinations of corresponding fractions of the several fractionations. Duplicate determinations of nitrogen were made on every sample and they agreed within ± 1.0 percent. Values for the D fractions are shown in Table I.

In native ovalbumin 6.9 percent of S_1 was removed by heating at 50° C. to give a total of 90.0 percent of the original protein remaining in the supernatant. An additional 8.2 percent protein was removed by heating S_2 for six hours at 60° C. Then, 22.8 percent more native protein was removed by heating S_3 at 68° C. for two hours. This would indicate that temperatures of 68° C. or above, would cause primary heat-damage to the ovalbumin molecules in addition to making the radiation-altered molecules insoluble at pH 4.85.

The irradiated ovalbumin samples, 15 ev/m, 30 ev/m and 60 ev/m showed a difference in the percent of the original protein solution remaining in the S_1 fractions. This was due to the difference in the percentage of protein removed in the D fraction as a result of denaturation directly due to irradiation. Regardless of the irradiation dosage, an additional 30.0 percent of the original material was removed when S_1 was heated for six hours at 50° C. When S_2 was heated for six hours at 60° C., the S_3 fraction showed an additional 10.0 percent loss of protein. The percentage of protein lost when S_3 was heated for two hours at 68° C. was more erratic. The ovalbumin which had absorbed 15 ev/m showed an additional 18.5 percent loss of protein. The 30 ev/m sample showed a loss of 24.7 percent protein. An average of 15.5 percent loss of protein was obtained when the S_3 fraction of ovalbumin which had absorbed 60 ev/m was heated for two hours at 68° C.

Serological tests

Serological tests were performed on the various supernatants and the D fractions. In both the measurement of the turbidity of the antigen-antibody complex and the measurement of the nitrogen content of the antigen-antibody complex, a decrease in serological activity was defined as a shift in the position of the precipitin curve along the antigen or the x-axis toward a region of higher protein concentration (Figure 5). As reported by Fricke, Leone, and Landmann (1957) a convenient measure of the relative serological activities of the solutions of irradiated ovalbumin and the several fractions derived from them is the ratio of the concentration of protein required to get the maximum reaction for native protein and that of any system being compared to it. This type of serological measurement is called, by them, "the ratio of the peaks."

Table IV contains values obtained from comparative turbidimetric tests of the fractions from several samples of irradiated ovalbumin. The shift of the I curve toward higher antigen concentrations was found to correlate directly with the irradiation dosage. The 30 ev/m samples gave an average N/I ratio of 0.748 with antiserum VB-2856; the 60 ev/m samples gave an average N/I ratio of 0.590 with the same antiserum. With antiserum VB-1057 the 30 ev/m samples gave a N/I ratio of 0.790; the 60 ev/m sample gave a N/I ratio of 0.640. With both the antisera a greater shift of the I curve towards higher protein concentrations was obtained with the 60 ev/m samples than the 30 ev/m samples. The variations in values obtained for the two antisera are primarily due to differences in their inherent precipitating capacities.

The greatest deviation of the serological curve from native ovalbumin was obtained with the D fractions. Of the supernatants, S_1 showed the greatest deviation in serological activity from native. When D was removed from solution, the position of the curve was shifted towards that of N, that is, to the left of the curve for I. In the series of supernatants obtained by heating S_1 up to ten hours at both 50° C. and 60° C., the serological ratios of the peaks tended to approach unity as the thermolabile molecules were removed from solution.

The values for the ratios shown in Table V were obtained from the determinations of nitrogen in the precipitates of serological tests. Solutions of gamma globulin derived from antisera were used as the antibodies in this series of tests. The N/I ratio could again be correlated with irradiation dosage. The 15 ev/m samples gave an average N/I ratio of 0.92; the 30 ev/m sample gave an average N/I ratio of 0.855; and the 60 ev/m samples gave an average ratio of 0.795. As the thermolabile components were removed, the N/S_1 and the N/S_2 ratios approached unity. The D fraction again showed the greatest deviation of serological activity from N as indicated by the N/D ratio of 0.042 to 0.115.

DISCUSSION

Thermal fractionation studies

The thermal fractionation studies showed that gamma irradiation produced a denaturation of some molecules in lyophilized ovalbumin. Other molecules were damaged to a lesser degree as was demonstrated by their increased thermal lability. With respect to the denatured molecules, the question could be proposed as to whether the amount of irradiation absorbed per molecule would correlate with the amount of irradiation. It was found that the quantity of D removed from solution was dependent upon both the irradiation dosage and the length of time after solvation before the D fraction was removed by centrifugation. If the system had absorbed an irradiation of 15 ev/m, 34.0 percent of the expected 15.0 percent of I was insoluble at the isoelectric point when the solution was allowed to stand for five minutes before centrifugation. Seventy-six and one half percent of the expected 15.0 percent of I was obtained when the irradiated ovalbumin remained at the isoelectric point fifteen minutes. In the sample which had absorbed 30 ev/m, 38.7 percent of the expected 30.0 percent of I was obtained on standing five minutes at the isoelectric point. After eighteen to twenty-four hours the entire 30.0 percent of I was recovered. In the ovalbumin samples which absorbed 60 ev/m, only 25.0 percent of the expected 60.0 percent denatured I was obtained when D was removed after five minutes. After fifteen minutes 37.0 percent of the expected recovery was obtained. Even after eighteen to twenty-four hours only 71.0 percent of the expected amount of denatured I was obtained.

Thus, gamma irradiation structurally so degraded some molecules that they were immediately insoluble at the isoelectric point. Irradiation also appeared to establish a dynamic system in which the molecules in solution were continuously being altered enough to become insoluble at the isoelectric point at increasing time intervals. The length of time necessary to obtain the expected yield of denatured molecules seemed to vary directly with the irradiation dosage. Whether or not the increase in amount of denatured protein with time is instituted by the ionization of the bound water in the ovalbumin molecule is not known. With solvation of irradiated, lyophilized protein this dynamic state would be effective until the entire 60.0 percent of the denatured molecules were recovered from the 60 ev/m samples.

During the process of lyophilization some of the native molecules were altered enough to be insoluble at the isoelectric point. This accounts for the D fraction that was found in the solutions of native ovalbumin.

In the heat-denaturation studies performed at pH 7.2 and pH 4.85, it was found that both the native and irradiated systems showed a greater denaturation at pH 4.85 than at pH 7.2. Gibbs (1952) found that heat-denaturation was considerably affected by alteration of the pH from the neutral point of water. He found that, as the pH of a solution was changed, there would be either ionization or suppression of the acidic or basic groups on the side chains which affect the stability of the molecule. The alteration of only one of the important groups could materially alter the reactivity of the molecule and could make it more sensitive to heat at the isoelectric point. Heating solutions of protein at pH 4.85 also resulted in the separation of labile components which were insoluble or only slightly soluble in water at pH 11.0 whereas the labile fractions obtained when the system was heated at pH 7.2 were soluble in water pH 9.0. The apparently irreversible denaturation produced by heating at pH 4.85 was probably due to the ionization of the basic or acidic side groups of the protein molecule. This ionization would result in the formation of more numerous sites to be affected by heat.

Serological studies

The precipitin curves of the D fractions were shifted far to the right along the x-axis because of decreased serological activity of D. After repeated dissolutions and reprecipitations of D, the ratio of N/ID averaged 0.056. The question can be asked as to whether D should retain any biological activity at all. It is quite possible that the serological activity remaining in D is due to contamination by trapped native molecules in spite of repeated washings.

The serological tests of the irradiated systems indicated that the alteration of the biological activity was due to two factors. The first factor was the denatured constituents formed during the irradiation of the ovalbumin sample. The whole irradiated solution, I, showed a greater deviation from the serological activity of native ovalbumin than any of the supernatants. There was a direct relationship between radiation dosage and the shift of the curve towards decreased reactivity (Tables IV and V). The greater the absorption of radiation the greater was the concentration of protein that was required to obtain the peak of the precipitin curve.

The second factor influencing serological activity was the partially denatured constituents identified as the thermolabile components. As these components were removed from solution, the ratio of the peak of the curve for N to the peaks of the curve for the supernatants approached unity.

The shape of the precipitin curves of the supernatants of the irradiated systems appeared to resemble the curve of the native system closely. Since the shape of the curve is dependent upon the reactivity of the combining groups of the molecule, it appears as if the serological activity is due to molecules which have not been altered during irradiation. The increased antigen concentration required for maximum antigen-antibody reaction is due to the presence of protein molecules with little or no reactivity.

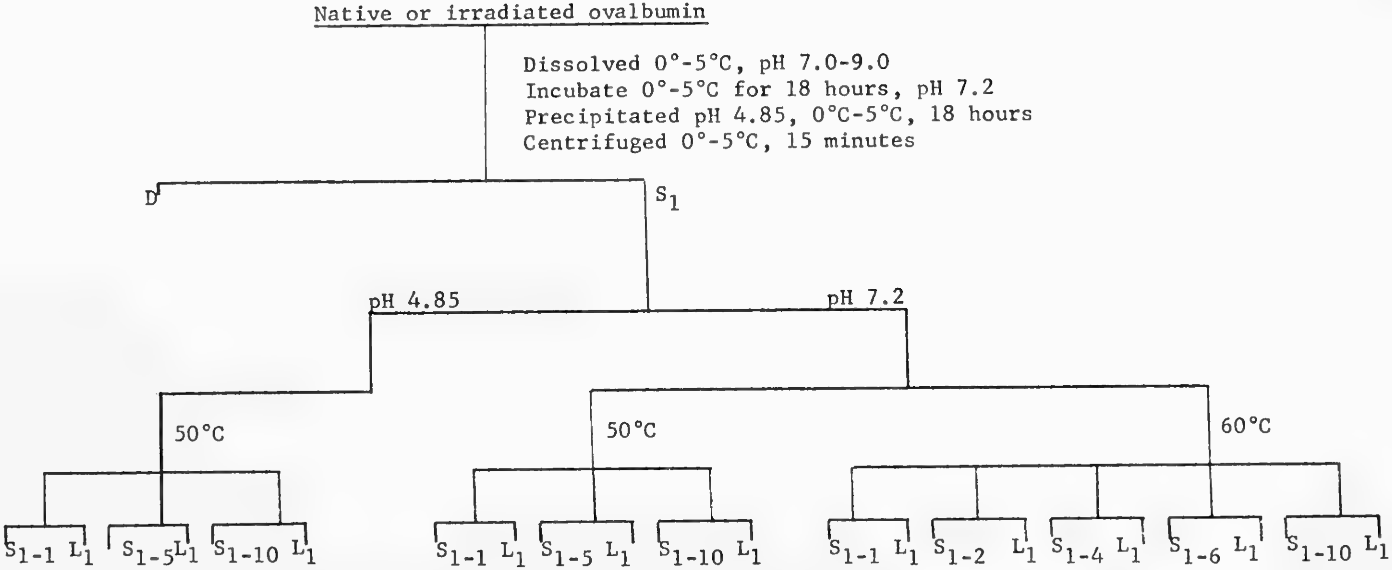
The specific combining groups for the antinative antibodies on the radiation-denatured molecules, D, were either completely destroyed or were present in such small amounts that little serological activity was noted. The protein structure of the thermolabile molecules was altered to a lesser extent than was the structure of the molecules in D. If the thermolabile molecules retained some of their specific groups, they could still combine with antibody molecules. Because of the destruction of a portion of the groups, a higher concentration of protein would be required to cause a precipitin reaction. The difference in combining capacity of the thermolabile molecules could cause the differences in the heights of the native and irradiated curves which were obtained in some instances. The differences in height were not consistent results and no correlations to either dosage or the amount of heat applied to the system were attempted. Information is needed on the nature of the combining sites of the modified molecules in irradiated ovalbumin in order to explain the mechanism whereby the shapes of the curves are alike but the heights of the curves are variable.

SUMMARY

Lyophilized ovalbumin irradiated with gamma rays so as to absorb 15, 30, and 60 electron volts per molecule of protein possessed molecules in various stages of structural degradation. The most severely damaged molecules precipitated at the isoelectric point of native ovalbumin. Less severely damaged molecules did not precipitate at the isoelectric point but exhibited different degrees of thermolability. The different stages of degradation of these thermolabile components were demonstrated by heatings at 50° C., 60° C., and 68° C. and then precipitating them at the isoelectric point.

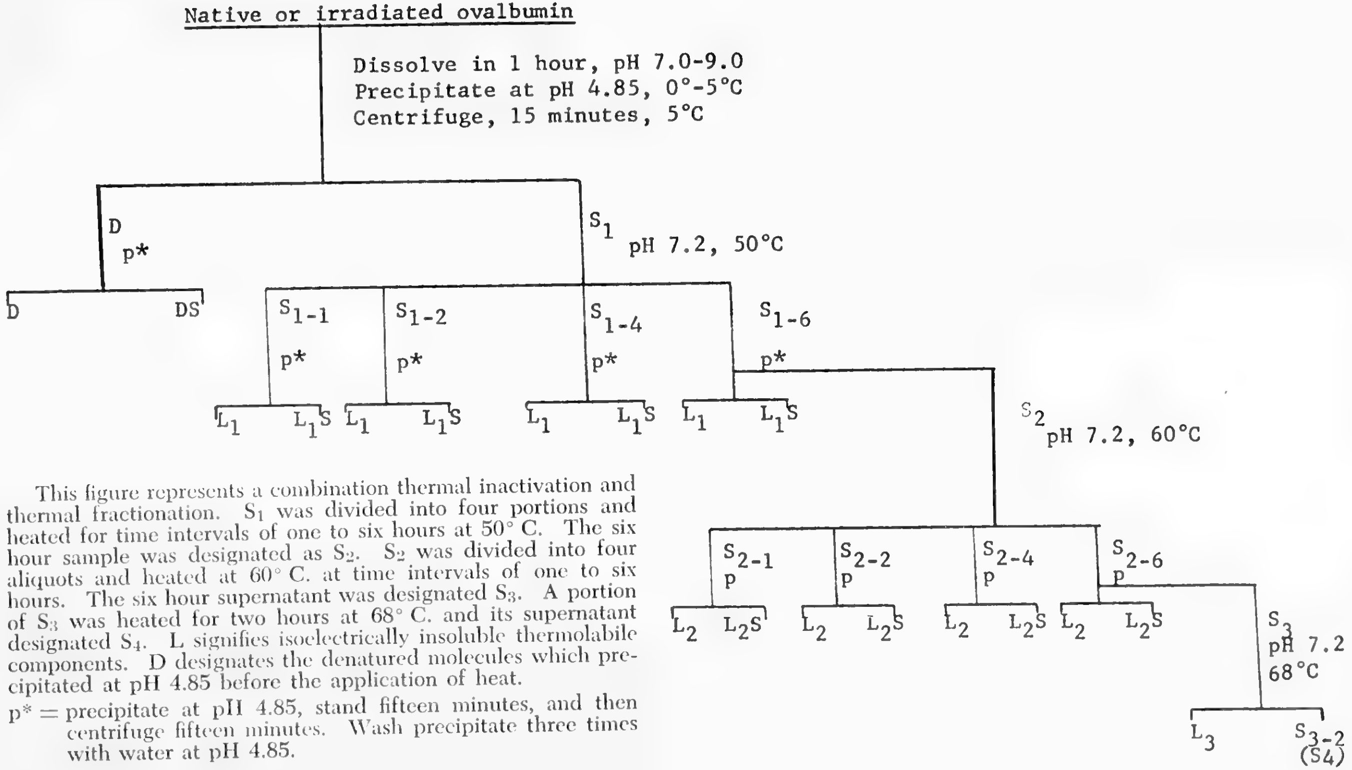
Serological testing provided a sensitive means of detecting alteration of the protein molecule by irradiation. As the irradiation-altered molecules were removed, the serological activity of the protein remaining in the supernatants tended to approach the serological activity of the native ovalbumin. Whether or not the denatured fraction retained any serological activity at all is questionable.

FIGURE 1



The thermal fractionations of the S_1 at 50° C. were performed at pH 4.85 and pH 7.2. The thermal fractionations at 60° C. were performed at pH 7.2 only. D was the protein which was insoluble at pH 4.85 prior to heating. S_1 was the protein solution of native or irradiated ovalbumin that was soluble at pH 4.85 before heating. The second subscript referred to the heating period. Thus, S_{1-5} indicated that S_1 was heated for a period of five hours. L_1 designates the material, after a period of heating, that was insoluble at pH 4.85.

FIGURE 2

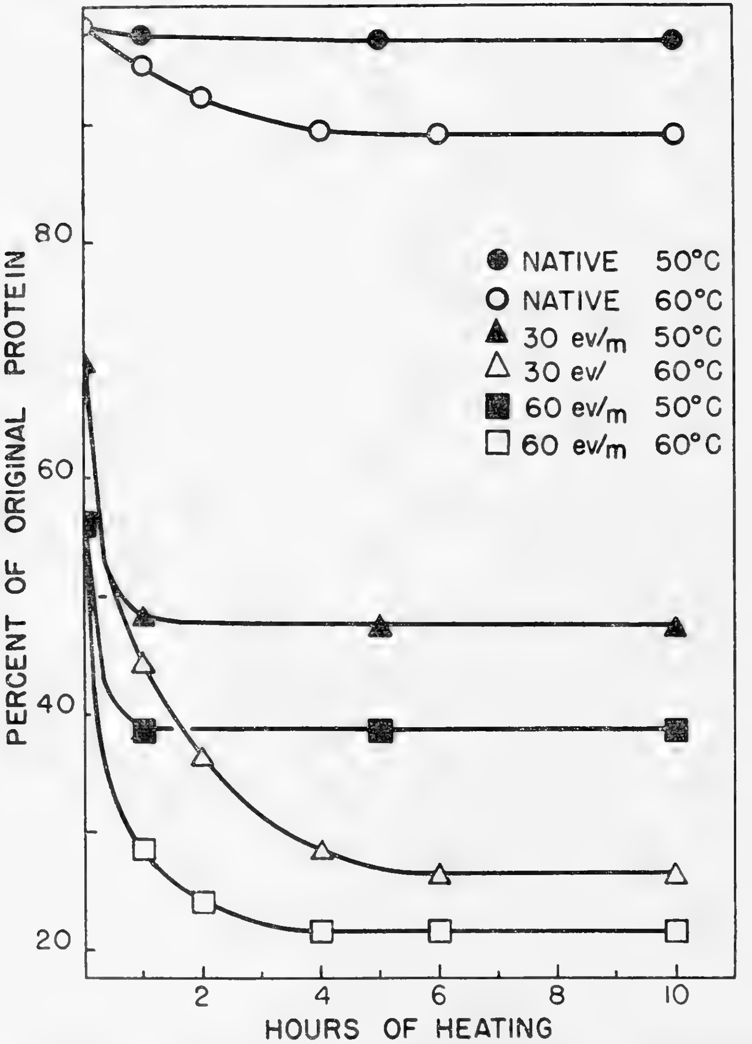


This figure represents a combination thermal inactivation and thermal fractionation. S_1 was divided into four portions and heated for time intervals of one to six hours at 50° C. The six hour sample was designated as S_2. S_2 was divided into four aliquots and heated at 60° C. at time intervals of one to six hours. The six hour supernatant was designated S_3. A portion of S_3 was heated for two hours at 68° C. and its supernatant designated S_4. L signifies isoelectrically insoluble thermolabile components. D designates the denatured molecules which precipitated at pH 4.85 before the application of heat.

p* = precipitate at pH 4.85, stand fifteen minutes, and then centrifuge fifteen minutes. Wash precipitate three times with water at pH 4.85.

FIGURE 3

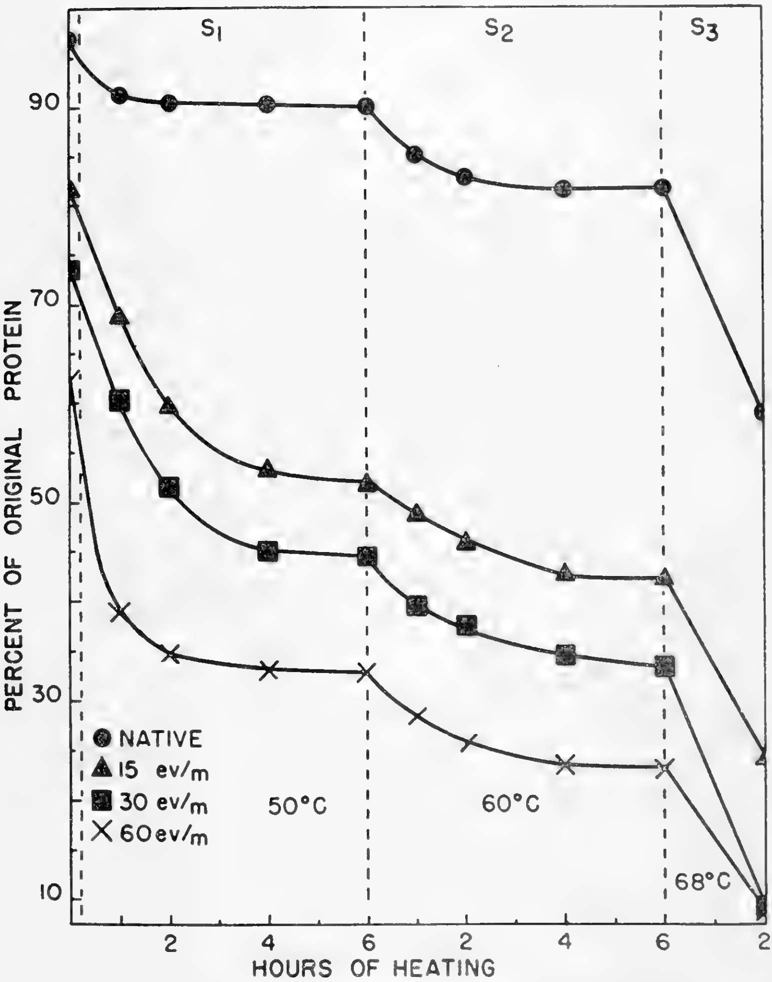
Effect of Temperature on the Isoelectrically Soluble Supernatant of Irradiated and Native Ovalbumin



Representative curves of the effect of temperature on the denaturation of lyophilized native and irradiated ovalbumin are illustrated. All values are expressed in terms of the percent of protein in the original solutions of irradiated or native ovalbumin. The abscissa represents the hours S_1 was heated. S_1 is plotted on the ordinate in terms of percentage of the original protein solution.

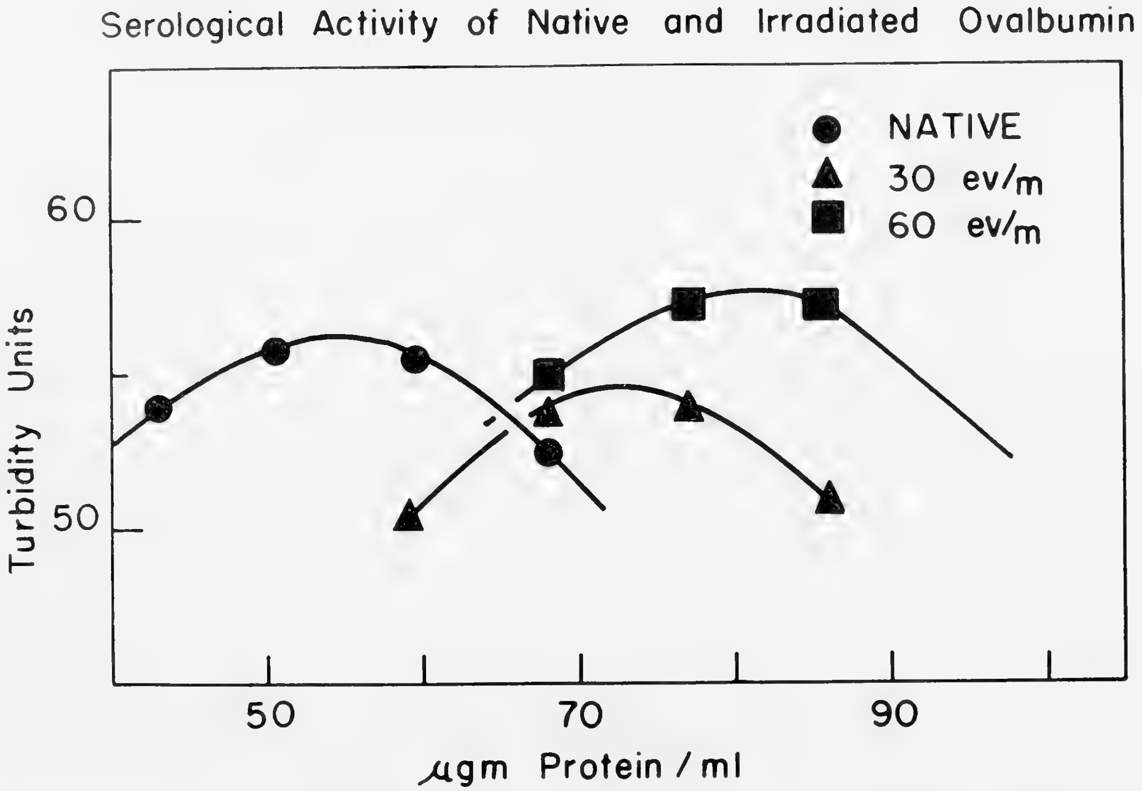
FIGURE 4

Thermal Inactivation of Isoelectrically Soluble Native and Irradiated Ovalbumin



These curves show the effect of heat on native and irradiated ovalbumin which had absorbed 15 ev/m, 30 ev/m, and 60 ev/m. The hours of heating at temperatures of 50° C., 60° C., and 68° C. are denoted on the abscissa. The three ordinates represent the S_1, S_2, and S_3 fractions. All values are calculated in terms of percent of protein in the original solutions of irradiated or native ovalbumin.

FIGURE 5



The 30 ev/m and the 60 ev/m samples of irradiated ovalbumin (I) produced a shift to the right along the x-axis toward higher protein concentrations. This indicates a decrease in serological activity from that on native ovalbumin (N). The shift from N is correlated with the absorption of gamma-ray energy. The 60 ev/m samples showed a greater shift from N than did the 30 ev/m samples.

TABLE I.—Relationship of time to the amount of protein that is insoluble at pH 4.85, the isoelectric point of native ovalbumin.

Sample	5 Minutes		15 Minutes		18–24 Hours	
	Percent N or I	Percent expected yield	Percent N or I	Percent expected yield	Percent N or I	Percent expected yield
Native	0.5	....	2.0	....	2.0	....
15 ev/m	5.2	34.7	11.5	76.5	....	....
30 ev/m	11.6	38.7	....	....	30.0	100.0
60 ev/m	14.8	25.0	22.2	37.0	45.0	71.0

Percent of N or I represents the percentage of the original protein which was removed at intervals of 5 minutes, 15 minutes, and 18 to 24 hours after adjustment of the solution to pH 4.85. Since 100 ev/m is required to cause an average of one ionization per molecule of lyophilized ovalbumin, it was assumed that an irradiation absorption of 15 ev/m, 30 ev/m and 60 ev/m would cause a corresponding 15 percent, 30 percent, and 60 percent denaturation of the ovalbumin molecules. The percentage of the denatured material which was obtained as D at the three time intervals was calculated as the percentage yield.

TABLE II.—Percent recovery of protein in fractions obtained from irradiated preparations of ovalbumin.

	Percent N or I				Percent S_1				Percent S_2				Percent S_3			
Sample	S_1	D	DS	Total	S_2	L_1	L_1S	Total	S_3	L_2	L_2S	Total	S_4	L_3	L_3S	Total
Native	96.9	0.48	1.8	99.2	91.3	1.5	1.7	94.5	92.4	3.6	3.7	99.8	17.4	5.2	2.2	24.8
15 ev/m	82.5	11.5	1.8	95.8	63.3	28.3	4.9	96.5	86.0	2.3	2.9	91.2	51.8	6.9	13.5	72.2
30 ev/m	73.5	11.6	13.7	98.8	59.8	31.7	4.7	96.2	75.4	22.8	3.8	102.0	25.4	12.5	1.8	39.7
60 ev/m	62.8	14.8	23.9	101.5	52.2	19.0	29.6	100.8	62.8	31.7	6.4	100.9	34.3	31.1	12.7	78.1

Data from individual experiments on three irradiation dosages are given to represent the percent of protein recovered from thermal fractionations. The values for S_1, D, and DS are the percentage of N or I recovered. The total percent of protein in the S_2 fractions, L_1, and L_1S forms the percent of the protein recovered in the S_1 fraction. In like manner the total percentage of protein in the S_3 fractions, L_2, and L_2S form the recovery in the S_2 fraction.

TABLE III.—Percent of the original protein found in the supernatants and the thermolabile components obtained from thermal fractionation.

Fraction	Native	15 ev/m	30 ev/m	60 ev/m
S_1	96.9 ± 1.6	82.0 ± 0.5	73.5	62.8 ± 2.0
S_2	90.0 ± 3.5	52.0 ± 0.2	44.0	32.7 ± 1.0
S_3	81.8 ± 7.6	42.7 ± 1.7	33.0	23.4 ± 2.2
S_4	59.0 ± 11.0	24.2 ± 0.9	8.3	7.9 ± 0.6
L_1	1.5 ± 1.0	28.3	31.7	19.0
L_2	3.6 ± 0.3	2.3 ± 1.1	22.8	31.7 ± 5.1
L_3	5.2 ± 3.5	6.9 ± 2.2	12.5	31.1 ± 5.0

The average results obtained from the thermal fractionation of native and irradiated ovalbumin are given. The values represent the percent of the original protein solution that remained in the various fractions. The variability shown is that obtained from replicate determinations of corresponding fractions of the several fractionations.

TABLE IV.—Relative serological activities of fractions derived from irradiated, lyophilized ovalbumin as compared to native ovalbumin.

Sample	Antiserum	N/I	N/D	N/S_1	50° C			60° C				
					N/S_{1-1}	N/S_{1-5}	N/S_{1-10}	N/S_{1-1}	N/S_{1-2}	N/S_{1-4}	N/S_{1-6}	N/S_{1-10}
30 ev/m	VB-2856	.748	.045	.785	.825	.855	.980	.844	.868	.889	.880	.890
30 ev/m	VB-1057	.790	.077	.845	.858	.915	.930	.873	.873	.873	.902	1.01
60 ev/m	VB-2856	.590	.059	.735	.805	.841	.935	.844	.935	.935	.968	.968
60 ev/m	VB-1057	.640	.081	.825	.890	.915	.967	.865	.868	.908	.938	1.02

These data are the ratios of the micrograms of nitrogen in native ovalbumin to the micrograms of nitrogen in the various fractions of irradiated ovalbumin which are required at the point of maximum turbidity in the antigen-antibody reaction. The two sets of data for 30 ev/m and 60 ev/m illustrate the different inherent combining power of the two antisera used. All values were determined from turbidimetric analyses of the precipitin reactions.

TABLE V.—Relative serological activities of ovalbumin fractions as determined by the Lanni procedure for analysis of the precipitin reaction.

Sample	N/I	N/D	N/S_1	N/S_2
15 ev/m	.920	.043	.942	.992
30 ev/m	.855	.115	1.02	1.04
60 ev/m	.795	.042	.964	.985

These data are the ratios of the micrograms of nitrogen of native ovalbumin to the micrograms of nitrogen of the various fractions of irradiated ovalbumin which were found to form the peak of the precipitin curves.

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A Seasonal Survey of the Vertical Movements of some Zooplankters in Leavenworth County State Lake, Kansas

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INTRODUCTION

In this work, analyses are made of the vertical distribution of nine species of arthropod plankters that were found in each of the first nine meters of water from collections made at dawn, noon, dusk, and midnight of one day in the months of June, August, and November, 1958, and March, 1959. Various explanations of vertical movements of zooplankters have been postulated (Juday, 1904; Russell, 1927; and Worthington, 1931). Although temperature, food, sex, size and many other factors have been found to modify the vertical migration of individuals in populations of zooplankters, most workers agree that the 24-hour cycle of subsurface illumination is the essential stimulus. The complex interrelationships of the factors causing movements of individuals of the same species in a lake must be determined before accurate explanations of seasonal variance in vertical movements can be made.

Cushing (1951) reviewed the literature on many of the aspects of vertical migration. Publications after 1951, concerning vertical migration, include studies by Bainbridge (1953), Hardy (1956), Hardy and Bainbridge (1954), Harris and Wolf (1955), and Knight-Jones and Qasim (1955). Only one year-round study of the vertical movements of zooplankters in the same lake has been made (Plew and Pennak, 1949).

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We wish to express our appreciation to Doctor Robert R. Sokal of the University of Kansas who made valuable suggestions regarding the statistical treatment of the data.

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* Now with Project Chariot, Kotzebue, Alaska.

GENERAL METHODS

Vertical series of plankton samples were taken on June 21-22, 1958, August 15-16, 1958, November 22-23, 1958, and March 1-2, 1959. Each vertical series consisted of samples taken in each meter from one through nine meters. The time required to obtain a vertical series varied from one to two hours. The sampling-time was bracketed around 6:00 a. m., 12:00 a. m., 6:00 p. m., and 12:00 p. m. Approximate terms were assigned to each sampling period (6:00 a. m. = dawn; 12:00 a. m. = noon; 6:00 p. m. = dusk; and 12:00 p. m. = midnight). A total of 36 samples was taken during each 24-hour period, resulting in an accumulative total, for the year, of 144 samples.

The collecting-apparatus consisted of a Clarke-Bumpus plankton sampler (Clarke and Bumpus, 1950, and Welch, 1948) with a No. 25 silk bolting net. The sampler was suspended by a cable from a derrick and was towed through the water at estimated speeds of 0.5 to 1.5 knots. Samples of plankton were obtained by towing the sampler through each meter for a period of one to two minutes. The smallest volume of water sampled at any depth was eight liters and the largest volume of water sampled at any depth was 608 liters.

After each haul, the concentrated plankton was transferred from the collecting cup to a bottle containing 95 percent alcohol, which diluted the 95 percent to 75 percent alcohol.

A Secchi-disk reading and a vertical series of temperatures and dissolved oxygen were taken on each sampling date.

Counts were made in the Hydrobiology Laboratory, University of Kansas, of the numbers of individuals of nine limentic zooplankter species. Each preserved sample was diluted to a known volume. The known volumes varied from 25-ml. for samples containing a small quantity of preserved plankton to a 150-ml. for samples containing a large quantity of preserved plankton. All dipteran larvae in each preserved sample were counted. The numbers of individuals of all species of Cladocera and Copepoda that were present in three 1-ml. portions of a diluted sample were counted in a Sedgewick-Rafter Cell, using a binocular microscope.

The average number of individuals per ml. of each species was determined from the three 1-ml. sample counts and was used to calculate the average number of individuals of each species per liter. The average number of individuals per liter for each species, for all liters sampled in each collecting period, was calculated and is summarized in Table I. These data indicate the population levels on which daily changes in vertical distribution are based. The average number of individuals per liter of each species in each meter, from one through nine meters, were summed. The sum was divided into the average number of individuals per liter at each depth, one through nine meters, and multiplied by 100 to find the percentage of the total population at each depth, for each species in each collection-period as illustrated in the following equation:

$$\frac{\text{average number per liter at any meter level}}{\text{sum of the average numbers per liter in nine meters}} \times 100 = \text{percent of population}$$

The results of the calculations are graphically represented in Figures 2 through 30.

The adults and copepodids of all Copepoda were grouped and considered as "adults." All nauplii and metanauplii were grouped and treated as a single category. Zooplankters were identified with the aid of keys by Pennak (1953), Ward and Whipple (1918), and Brooks (1957). Other plankters were identified with keys by Smith (1950).

Ten-ml. portions from each preserved sample were placed into vials containing two ml. of glycerin and stored for permanent reference.

ANALYSIS OF SAMPLING TECHNIQUE

Since the population estimate of each species in each preserved sample was based on counts per milliliter taken from the sample, an analysis was made in order to determine the number of such samples necessary to reasonably estimate the population of each species in a sample.

The samples collected at midnight at one and six meters and at noon at one and six meters on June 21-22, 1958, were selected for analysis. The samples were chosen in order to present as great a range as possible in the numbers of each species. All individuals of *Daphnia galeata mendotae, Bosmina longirostris, Diaptomus pallidus,* and *Mesocyclops edax* in each of ten one-milliliter subsamples from each preserved sample were enumerated.

An inspection of the counts indicated that the mean was correlated with the variance. A rankit analysis disclosed leptokurtosis (Fisher and Yates, 1953). Square-root transformations of the counts were used to reduce kurtosis. An analysis of variance of the transformed counts of each species was made. The F value for each species was highly significant (Table 2).

Because of the amount of time necessary to count the individuals in a one-milliliter sample, three one-milliliter counts were chosen as being the maximum practical number that could be done. The five percent confidence interval of the mean for three counts was calculated from the formula $i = \frac{t \times s}{n}$, where i = interval, t = t value at .05 (d.f. = 2), s = the square root of the mean square for individuals from Table 1, and n = the number of counts. Since four species were counted from each of four samples, a total of 16 intervals was calculated.

The accuracy of estimating the population based on a mean of the individuals in three one-milliliter counts was tested empirically as follows. The mean of three randomly selected counts was determined for each of the four species in each of the four samples, resulting in a total of 16 means. Sixteen population estimates were determined using the means of three counts and the means of ten counts. The remaining samples for noon and midnight of June 21-22, 1958, were processed using a mean of three counts to estimate the population and Figures 2, 11, 15, and 19 were constructed. In no case except for *Daphnia galeata mendotae* at noon did the population estimate based on the means of ten counts make a difference in the general shape of the figure for noon or midnight for any of the four species. The estimate of the population of *Daphnia galeata mendotae* at one meter, based on the mean of three counts, was much higher than the estimate of the population based on the mean of ten counts. Even so, this did not obscure the concentration of the population at three meters and did not affect the subsequent evaluation of the pattern of movement for June 21-22.

Because of the results of the above analysis, three counts were deemed sufficient to demonstrate the population shifts associated with vertical migration. Minor variations in the shapes of Figures 2 through 30 were not considered. It seems probable that major shifts in the population of each species were readily detected, but minor shifts may have been missed.

Clogging of the net is a hazard often encountered when a fine-mesh net is used. Yentsch and Duxbury (1956) found that the clogging of the net causes the calibration-value to decrease until the rate-of-flow through the meter approaches the frictional forces brought about by the metering mechanism. In the present study, on August 15-16, 1958, sampling was hindered. A thorough examination of the collecting apparatus revealed no deficiency in its mechanics, indicating that the sampling trouble was probably due to the clogging of the net. A planktonic analysis revealed that a high bloom of *Coelosphaerium*, a spherical colonial alga, was present. The size of most colonies ranged between 15 and 65 microns in diameter, as determined by measurements with a calibrated ocular micrometer. The mesh of a No. 25 silk bolting net is 64 microns in diameter when the net is new. After the net has been used to obtain samples, the mesh is reduced slightly through shrinkage. Organisms which are larger than 64 microns diameter pass down the inside surface of the net to the collecting cup. Organisms smaller than 64 microns diameter pass through the mesh. If organisms are only slightly smaller or larger than 64 microns on any axis, they can wedge into the mesh and clog the net. As a general rule, tows were of short duration and at slow speeds in order to reduce the error created by the clogging of the net. Deviations from the assigned calibration value, due to resistance and clogging, increased as a function of towing velocity (Yentsch and Duxbury, 1956). No statistical correction factor for the error caused by clogging of the net was applied.

THE STUDY AREA

Leavenworth County State Lake, located approximately four miles northwest of Tonganoxie in Leavenworth County, Kansas, was impounded in 1931. A dam was placed across a valley below the confluence of two intermittent streams which now form two major arms of the lake. The lake has an area of 175 acres, a capacity of 3,932 acre-feet, and a maximum depth of 17 meters (Stene, 1946). In 1958, the areas that were deeper than nine meters were not extensive enough to permit operation of the sampler below that level. Drainage from approximately 2,500 acres passes water into the lake through several small creeks, of which two tributaries that flow into the ends of the arms of the lake are most important. The areas drained consist of woodlands, fields, and some prairie. The lake remains clear most of the time. It becomes turbid only after intense rains.

When excessive water comes into the lake, a valve in the dam is opened and the water is discharged from the bottom. If a permanent thermocline is present during the discharge, it is dropped approximately the same depth that the level of the lake is lowered. The temperature in June, 1958, was 77° ± 1.9° F. to a depth of five meters where a permanent thermocline existed. The temperature lowered to 49° ± 1.6° F. at ten meters where it again was constant to thirteen meters, the lowest depth measured. In August, 1958, heavy rains raised the level of the lake. Several feet of water were drained from the bottom of the lake. The permanent thermocline dropped from the fifth to the eighth meter (Table 3). The heavy rains and the turbulence caused by the draining disturbed the water above the eight-meter level, resulting in the temperature gradient illustrated in Figure 1.

The area studied in the lake extended northeast from the spillway for approximately 500 yards.

ACCOUNTS OF SPECIES

Daphnia galeata Sars, 1864, *D. g. mendotae* Birge, 1918, N. Comb.

June 21-22, 1958. Figure 2.

The largest percentage of the population remained in the upper five meters during the day. The population was randomly distributed through the epilimnion at midnight. The concentration of the population near the surface was greater at dawn and dusk than at noon, indicating that a slight downward movement occurred between dawn and dusk. Evidently the migratory movement of most of the population was a basic response of positive phototaxis because, at night, the population became randomly distributed. However, there was a downward movement of a small part of the population at noon that was probably caused by the high light intensity at that time of day.

August 15-16, 1958. Figure 3.

The bulk of the population was in the third meter at dawn, in the fourth meter at noon, and in the fifth meter at dusk. The population was randomly distributed above the thermocline at midnight. Seemingly most of the population reacted negatively to light, showing a response opposite to that of most of the June population. This change could be a result of the increase in temperature from 77° ± 0.4° F. in the upper four meters in June to 86° ± 2.4° F. in the upper four meters in August (Table 3). High temperatures increase negative phototaxis, whereas low temperatures lessen or even reverse negative phototaxis (Welch, 1952: 251).

More than 90 percent of the population remained above the six-meter level in all four sampling times. This distribution is probably accounted for by the decrease in oxygen values below the six-meter level. The oxygen concentrations dropped from 9.0 mg./l. in the first meter to 0.2 mg./l. in the sixth meter (Table 3). Some cladocerans have been reported (Thienemann, 1919; Grover and Coker, 1940; and Kikuchi, 1930) unable to pass through a thermocline, but the population of *D. galeata mendotae* in June was little affected by the thermocline, thus supporting the assumption that in August this species was limited to the upper six meters by an oxygen deficiency in the water below that level.

November 22-23, 1958. Figure 4.

The population was randomly distributed at each of the four sampling times. Either taxic responses had disappeared, or, more likely, the individuals of the population were unable to swim against the currents created by the autumnal overturn.

March 1-2, 1959. Figure 5.

Much of the population was concentrated near the surface at each of the four sampling times. This distribution indicates that the population was responding negatively to gravity. A negative geotaxic response does not explain why the population maintained itself near the surface against the currents of the spring overturn when the November population did not. The phenomenon might be explained by a change in the ratio of adults to young. Most cladoceran populations in temperate zones apparently do not reproduce during the winter. Therefore, the early spring populations are mostly adults. Adult cladocerans are able to swim against currents better than young. If an adult population reacts negatively to gravity, there is a good possibility that a high percentage of such a population could maintain itself in the upper strata in spite of an overturn.

There was a slight downward movement of part of the population at noon that was probably caused by the high light intensity at that time of day.

Remarks

No previous work on the vertical migration of zooplankters in freshwater has utilized the new designations for species of *Daphnia* as listed by Brooks (1957). Any correlation of the vertical movements of *D. galeata mendotae* must be made with older designations of the species *D. "longispina."*

Langford (1938), working in Lake Nipissing, Toronto, Canada, found concentrations of *D. "longispina"* near the surface at night and in deeper water during the day, in the period June to September, 1934. *D. galeata mendotae* could be the same species referred to by Langford because *D. galeata mendotae* is one of the species named from the *D. "longispina"* complex by Brooks (1957), and the range extension of *D. galeata mendotae* covers the large northern lakes where Langford worked. Plew and Pennak (1949), working in an Indiana lake, found *D. "longispina"* was abundant only in January and April of 1942, and although small numbers of individuals of this species appeared in other seasonal samples, there was some indication that vertical migration, similar to that reported by Langford, occurred year-round. The distribution patterns of *D. "longispina"* populations, which were reported for the summer by Langford and reported for the year-round by Plew and Pennak, were similar to only the daytime distribution of *D. galeata mendotae* in August, of the present study. The seasonal changes in temperatures that were found by Langford and by Plew and Pennak had no significant effect on the migratory responses of *D. "longispina."*

Daphnia pulex Leydig, 1860 Emend. Richard, 1896

November 22-23, 1958. Figure 6.

The population was randomly distributed at each of the four sampling times, probably due to autumnal overturn.

Remarks.

Only in collections taken in November was *D. pulex* abundant enough for an analysis of vertical distribution. This species was identified in samples taken in other collection periods, but was rare.

Any correlation of the vertical movements of *D. pulex* with previous accounts meets with the same kind of nomenclatural problems discussed for *D. galeata mendotae.* The older species, in this instance, are from the *D. "pulex"* complex.

Brooks (1957: 66) states, "*Daphnia pulex* is principally a pond-dweller although it establishes populations in lakes with a fair frequency. In lakes, it usually occupies deeper waters during the day, tending to come nearer the surface at night." If vertical migration was occurring in the *D. pulex* population of Leavenworth Lake in November, 1958, it was obscured by the autumnal overturn.

Ceriodaphnia lacustris Birge, 1893

August 15-16, 1958. Figure 7.

Most of the population remained above the six-meter level at each of the four sampling times. Vertical migration of the population from the third and fifth meters toward the surface started between noon and dusk. The greatest concentration of the population at the surface occurred at midnight. Between midnight and noon, the population migrated downward to the third and fifth meters.

The presence of the thermocline and/or the deficiency of oxygen below the six-meter level restricted the population to the epilimnion. Apparently the basic response of this species was negative geotaxis that was modified by light so that the population was deepest during the time of greatest light intensity.

Remarks.

Several studies of vertical movement in *Ceriodaphnia* have been made. Steuer (1902) found higher concentrations of *C. pulchella* near the surface on nights when the moon was shining brightly. Worthington (1931) found that *Ceriodaphnia sp.* continued its upward vertical migration for several hours after sunset. The present study confirms the observations of Steuer and Worthington, and supports the hypothesis that light is a factor affecting vertical migration in this genus.

Thienemann (1919) found populations of *Ceriodaphnia sp.* restricted to the area above a thermocline. However, it is not known if Thienemann considered only the effect of the thermocline, or if he considered a possible oxygen deficiency.

Diaphanosoma brachyurum (Liéven) 1848

June 21-22, 1958. Figure 8.

Part of the population was near the surface at dawn, but a larger percentage was in the fifth meter. Most of the population was confined to the fifth meter at dusk. By midnight, most of the population was concentrated in the first and third meters.

Small numbers of individuals appeared in the dawn, dusk, and midnight samples (Table 1). The noon population was insufficient for an analysis of the vertical distribution. Since the sample collected from the sixth meter was the only one in which the species was taken at noon (0.03 individuals per liter), this indicates that the population remained in the deeper part of the epilimnion in the middle of the day. Most of the population was restricted to the epilimnion at all four sampling times, evidently by the thermocline.

Possibly the factors that affected the migration of *C. lacustris* in August were acting on *D. brachyurum* in June.

August 15-16, 1958. Figure 9.

The population was greater in the lower part of the epilimnion in the day. A large part of the population occurred near the surface at midnight. Most of the population was restricted to the epilimnion at all four sampling times.

Possibly the same factors that affected the downward migration in June were effective in August.

November 22-23, 1958. Figure 10.

The population was randomly distributed at each of the four sampling times. Seemingly this population was unable to swim against the currents created by autumnal overturn.

Remarks.

The migration of individuals of this species to the surface at night and into deeper water during the day has been reported by previous workers (Kikuchi, 1937; Thienemann, 1919; and Worthington, 1931). This report confirms their work.

The populations of *D. brachyurum* found in the June and August samples of the present study were unable to swim through a thermocline. However, Grover and Coker (1940) and Kikuchi (1930) found that *D. brachyurum* migrated through a thermocline and moved toward the surface at dawn.

Too little information is available to draw any conclusions as to why different populations behave differently with respect to the thermocline.

Bosmina longirostris (O. F. Muller) 1785

June 21-22, 1958. Figure 11.

Much of the population migrated from the lower part of the epilimnion towards the surface between dawn and noon, and moved back into the lower part of the epilimnion between noon and dusk. The population was randomly distributed above the thermocline at midnight.

The migratory pattern of the population of *B. longirostris* can be correlated with the 24-hour cycle of light. As the light intensity increased during the day, the population in the epilimnion moved up, and as the light intensity decreased in the evening, the population moved down. In the absence of light, the population became randomly distributed in the epilimnion. This type of migratory movement indicates that the population was displaying a positive phototaxic response in high intensities of light and a negative phototaxic response in low intensities of light. The restriction of the population above the six-meter level probably resulted from the presence of a thermocline rather than from a deficiency of oxygen, because dissolved oxygen was adequate below the six-meter level (2.5 mg./1. in the eighth meter).

August 15-16, 1958. Figure 12.

Many individuals remained near the surface during the day. The highest concentration of the population near the surface occurred at midnight. Most of the population remained above the five-meter level at the four sampling times.

Part of the population moved down at noon, indicating at least a partial reversal of the reaction to light from that shown in June. This type of movement is consistent with the interpretation of the effects of temperature on the reactions to light as given in the species account of *D. g. mendotae*. Evidently most of the population reacted postively to light.

November 22-23, 1958. Figure 13.

The somewhat scattered distribution of the population (probably a result of autumnal overturn) and the low numbers of individuals represented in the collections taken on this date (Table 1) make any interpretation of the diagrams in Figure 13 impractical.

March 1-2, 1959. Figure 14.

Most of the population was randomly distributed at each of the four sampling times, perhaps because of the spring overturn. Slightly larger concentrations of the population occurred near the surface at dusk and midnight, indicating that part of the population might have been responding negatively to gravity, and were able to swim against the currents of the spring overturn.

Remarks.

Some authors have stated that the *B. longirostris* was unable to cross a thermocline (Kikuchi, 1930 and Thienemann, 1919). *B. longirostris* is a relatively small zooplankter in comparison to other Cladocera and Copepoda that have shown migration through a thermocline, indicating that size may be a major factor in determining swimming ability.

Few accounts of *B. longirostris* have been published, and none concerning vertical movements showed results comparable to those found in the present study.

Diaptomus pallidus Herrick, 1879

June 21-22, 1958. Figure 15.

Although much of the population was randomly distributed at each of the four sampling times, there was some concentration near the surface during the day, and in the thermocline both day and night. An analysis of the population in the upper and lower meters revealed that most migrants were adults. The copepodids were randomly distributed. Throughout the day, more males than females moved toward the surface. Both males and females were concentrated in the lower meters at night.

Apparently most males reacted positively to light and most females reacted negatively to light. Both sexes moved down, or sank, to deeper water at night, perhaps indicating that both were reacting positively to gravity.

The concentrations of adults and copepodids in the thermocline at the four sampling times indicate that some individuals of the populations were less able to swim through the thermocline than others.

August 15-16, 1958. Figure 16.

Most of the population was restricted to the epilimnion, probably because of the decrease in oxygen below six meters (Table 3). There were slightly higher concentrations of the population near the surface at dawn and dusk than at noon. The population was randomly distributed at midnight.

At dusk, concentrations of the population occurred both near the surface and at the five-meter level. An analysis of the individuals near the surface and at depths of four and five meters revealed that more adults than copepodids were near the surface, and more copepodids than adults were in the fourth and fifth meters. The population at dawn, noon and midnight did not show an adult-copepodid separation. There was no indication that males and females underwent different reactions.

Seemingly the adults and copepodids responded to light in opposite fashions. Most of the adults reacted positively to light, and most of the copepodids reacted negatively to light. However, the greater number of adults near the surface at dusk than at noon indicates that some adults reacted negatively to light.

November 22-23, 1958. Figure 17.

The adults and copepodids were randomly distributed at dawn, dusk, and midnight. A slightly larger concentration of the population occurred near the surface at noon.

An analysis of the individuals in the upper and lower meters at noon revealed that more adults than copepodids were near the surface. The copepodids were randomly distributed. Evidently both sexes of adults responded to high intensities of light, and swam toward the surface in spite of the overturn. Any response to a taxic influence by the copepodids was apparently overcome and obscured by the overturn.

March 1-2, 1958. Figure 18.

A large part of the population remained near the surface at all four sampling times. Obviously much of the population was able to swim against the currents created by the vernal overturn, and was perhaps reacting negatively to gravity. During this time of the year, most of the individuals are adults; hence, they are better able to swim against currents.

Remarks.

Migration patterns have been found for several species of *Diaptomus*. Worthington (1931) found that *D. gracilis* and *D. leptopus* crossed a thermocline. Maloney and Tressler (1942) reported that only part of a population of *D. gracilis* moved through a thermocline. Thienemann (1919) found that *D. gracilis* remained above a thermocline. The reports cited above show that different populations of the same species can react differently to the same factor. *D. pallidus* in the present study moved through a thermocline and was restricted to the area above the thermocline when oxygen values in the hypolimnion were low. It would be interesting to know if *D. pallidus* in other areas swims through a thermocline, but no previous reports on the vertical migration of this species have been published.

Worthington (1931) reported that the young of *D. gracilis* remained in deeper water during the night when the adults were near the surface. Langford (1938) reported that adult males of *D. minutus* were deep during daylight at the same time the adult females were near the surface. The adult males moved up during the night and the adult females moved down. Plew and Pennak (1949) found that *D. birgei* migrated toward the surface at night and into deeper water during the day. The same migratory pattern was observed the year-round. Juday (1904) found that the migration of *Diaptomus* sp. was independent of any "degree of transparency" of the water. None of these reports cited above mentions an example of migratory movement, that is wholly in agreement with the migratory movements found for *D. pallidus* in the present study. The separation of the sexes of *D. pallidus* was the opposite of that found by Langford for *D. minutus* in that only the adult males of *D. pallidus* migrated. *D. pallidus* did not exhibit a year-round migratory pattern as Plew and Pennak (1949) reported for *D. birgei.* The separation of young and adults of *D. pallidus* did not occur at night as Worthington reported for *D. gracilis.*

Mesocyclops edax (S. A. Forbes) 1891

June 21-22, 1958. Figure 19.

A large percentage of the population remained in the lower strata throughout all four sampling times. An analysis of the individuals in the first and second meters and in the seventh, eighth and ninth meters revealed a random distribution of adults and copepodids (adults were most abundant).

There is an indication that part of the population in the lower strata was reacting negatively to light. The intensity of light at noon may have been strong enough to affect the population in the deeper water, inasmuch as the light penetration as based on a Secchi-disk reading was greater in June than at the time of any other collection.

Most of the population was restricted to the fifth through the ninth meter, seemingly by an inability to swim through the thermocline. The part of the population that remained below the thermocline may have been reacting postively to gravity.

August 15-16, 1958. Figure 20.

The bulk of the population was in the water above the five-meter level at the four sampling periods, probably due to the presence of the thermocline and the deficiency of oxygen in the hypolimnion. At dawn, the population reached its greatest concentration at the three-meter level, had moved into the four and five meter levels by noon, was concentrated in the fifth meter at dusk, and had started to migrate toward the surface at midnight. Most of the population apparently reacted negatively to light.

November 22-23, 1958. Figure 21.

Most of the population was randomly distributed at all four sampling times. There were slightly larger concentrations in the upper four meters both day and night. Evidently the autumnal overturn created currents against which most of the population could not swim. The part of the population which could swim against the currents seemingly reacted negatively to the influence of gravity.

Remarks.

Most published reports of vertical migration of "shorthorn" Copepoda have pertained to the *Cyclops* group. Any report of the literature concerning vertical movements that may be related to those found in *Mesocyclops edax* will be discussed in remarks under *Cyclops bicuspidatus.*

Cyclops bicuspidatus Claus, 1857

March 1-2, 1959. Figure 22.

Most of the population remained randomly distributed at the four sampling times. Slightly greater numbers of individuals remained near the surface both day and night.

An analysis of the population in the upper and lower meters revealed that more adults than copepodids were near the surface. A geotaxic influence and a change in the ratio of adults to young were the two factors that affected the migration of the population of *Daphnia galeata mendotae* in March. The same factors may have affected the migratory pattern of some of the individuals of *Cyclops bicuspidatus.*

Remarks.

Langford (1938) experimentally proved that *C. bicuspidatus* showed a positive phototaxic response at low temperatures. In Lake Nipissing, Toronto, Canada, in the period June to September, 1934, he found that the *Cyclops* group, which included *C. bicuspidatus, C. viridis,* and *Mesocyclops obsoletus,* were near the surface at night and in deeper water during the day. Maloney and Tressler (1942) reported that *C. bicuspidatus* was in deeper water at night and near the surface during the day, and that it migrated through a thermocline. Plew and Pennak (1949) found populations of *C. bicuspidatus* near the surface at night and in deeper water during the day, a daily migratory pattern that was the same the year-round.

The results found in published reports on migration in the *Cyclops* group and the results of the present study, which included *M. edax* and *C. bicuspidatus,* show that the *Cyclops* group has several patterns of vertical movement. Too little evidence has been accumulated on the migratory movements of the *Cyclops* group to explain the differences in the patterns.

Nauplii-mentanauplii of the Copepoda

June 21-22, 1958. Figure 23.

The population was extended from the first through the ninth meter and a larger concentration of the population occurred at the five-meter level at the four sampling times.

Nauplii and metanauplii stages are quite small and have little swimming ability. This small size may prevent movement through the thermocline and may partially account for the concentration therein.

August 15-16, 1958. Figure 24.

The population remained above the five-meter level at the four sampling times apparently because of the deficiency of oxygen below the five-meter level.

The vertical distribution and the migratory pattern of the nauplii and metanauplii were similar to that of the adults and copepodids of *M. edax* in August (Figure 20). The same factors that modified the migratory pattern of *M. edax* may have been acting upon the nauplii and mentanauplii population.

November 21-22, 1958. Figure 25.

The population was randomly distributed at all four sampling times.

March 1-2, 1959. Figure 26.

The population was randomly distributed at all four sampling times.

Remarks.

Langford (1938) found no marked diurnal movement in the nauplii of the Cyclops group, which he studied in Lake Nipissing, Toronto, Canada. Steuer (1902) showed experimentally that the nauplii and young of Cyclops came to the surface more readily than did the adults. Plew and Pennak (1949) found that the nauplii of *D. birgei* and *C. bicuspidatus* were nearer the surface during the day than at night.

The nauplii-metanauplii stages in the present investigation displayed migratory movements only in August that were the reverse of the patterns described by Plew and Pennak (1949).

Chaoborus (= *Corethra*) *punctipennis* (Say) 1823

June 21-22, 1958. Figure 27.

A small part of the population occurred above the nine-meter level during the day (Table 1). A larger percentage of the population moved toward the surface between dusk and midnight. Although individuals moved through the thermocline, there were slightly larger percentages of the population in the thermocline, indicating that passage through the thermocline was hindered.

The larvae of this dipteran remained in the water below the nine-meter level and above the bottom muds or in the bottom muds during the day; hence, the individuals that were taken in collections made during the day represented only a small portion of the total population.

August 15-16, 1958. Figure 28.

The pattern of migration was generally the same as for the June population except that there was a greater extension of the population toward the surface during the day. Larger percentages of the population occurred at the level of the thermocline in the daytime.

November 22-23, 1958. Figure 29.

The largest concentrations of the population near the surface occurred at dusk and midnight. Most of the population was below the fifth meter at dawn and noon, but a large percentage extended toward the surface throughout the day.

March 1-2, 1959. Figure 30.

The population was absent from the first nine meters at dawn, noon, and dusk, but extended toward the surface at midnight. Juday (1921) found that full-grown larvae remained in the bottom muds during the day. Most of the larvae that overwinter in temperate zones are full-grown, which might account for the absence of the larvae above the bottom in the March collections taken during the day.

Remarks.

Juday (1921) found that full-grown larvae of *C. punctipennis* which moved to the upper strata at night, moved to the bottom and well before the sun rose. Eggleton (1931) found that the migratory pattern of larvae in a lake covered by enough ice and snow to exclude a "considerable portion" of the light, was the same as the migratory pattern when the lake was clear.

Juday (1921) stated, " . . . the larvae of *Corethra punctipennis* give a prompt negative reaction to light . . ." He found, in addition, that larvae that were less than one-third as large as full-grown larvae remained in the waters above the bottom during the day whereas the full-grown larvae remained in the mud in the daytime. Both the small and the large larvae migrated towards the surface at night.

The factors that modify the migration of *C. punctipennis* larvae are not known. Migration occurs the year-round in larvae of widespread areas, and in a relatively consistent pattern. The data for *C. punctipennis* larvae in the present study indicate that the pattern of migration changes with the maturation of the larvae. Most of the evidence for the migratory patterns in this species supports the assumption that an endogenous diurnal rhythm may play a larger role than external stimuli, especially in mature larvae. Sudden changes in the external stimuli may produce an exogenous rhythm that lasts for a short time.

Exogenous rhythms that affected the migratory patterns of *C. punctipennis* larvae in Leavenworth County State Lake were produced by seasonal changes in light. Different migratory patterns appeared at each season. There was a great increase in the nummer of individuls per liter after dusk in June. However, the number of individuals per liter in August and November was about the same for dusk and midnight (Table 1). This phenomenon indicates that an earlier upward movement occurred in the evening in August and November than in June. This movement can be correlated somewhat with the reduced Secchi-disk reading of August and November as compared to June (Figure 1). The percentage of the population in the upper strata was greater in November when the light penetration was the lowest.

The data cited above support the hypothesis that light modified the migration of the larvae of *C. punctipennis.*

DISCUSSION

Cushing (1951) listed age, phytoplankton abundance, sunlight, temperature, and other weather phenomena as major factors that may modify migration. Welch (1952:242, 248) includes gravity and sex as major factors. More recently, Hardy (1956: 210) speculated on the effect of poisonous substances, which might be produced by phytoplankton and thus exclude some susceptible zooplankters from areas of dense phytoplankton. There are other minor factors that may modify migration. The complexity of any study of migration is well illustrated if only the major factors are considered. Any attempt to account for migration must be based on an intensive study of many of the factors listed above. Few accounts have been published in which more than one or two of the possible modifying factors were considered.

This study was made primarily to determine the seasonal migratory patterns of some larger zooplankters in Leavenworth County State Lake. Each collection was made on a date that corresponded to a different season. Hence, the differences in the factors that modified migration from one collecting date to another, were considered as seasonal changes. The more apparent environmental and biological factors that are known to modify migration, were correlated with the actual migratory patterns shown by the zooplankters. The factors that may have modified the migration of vertical distribution of each species are summarized in Table 4.

No attempt was made in this study to correlate the year-round distributional-patterns of each species to temperature, because too little data were accumulated and because daily fluctuations in temperature have been experimentally proven to have little effect on the daily migratory movements of zooplankters (Hardy, 1956: 201). Temperature was considered a factor only in those cases where it may have modified the response of zooplankters to light (*Daphnia galeata mendotae* and *Bosmina longirostris* in August).

Light was the most important factor which modified migration on June 21-22 and August 15-16, 1958. The amount of dissolved oxygen and the location of the thermocline greatly influenced the vertical distribution of the zooplankters in June and August. On November 22-23, 1958 and March 1-2, 1959, the overturn and the size of the plankters were most important in determining migratory patterns (Table 4).

In the remarks under the descriptions of the patterns of individual species, it was frequently mentioned that changes in vertical distribution were not found in November and March, although other workers had reported such changes. These differences may have resulted because we did not collect samples under the ice when the lake would be calm, but only when the lake was circulating. Thus, we may have missed winter migratory patterns.

There were also factors other than those listed in Table 4 that influence the migratory movements of the zooplankters. One example of such a factor might be the predator-prey relationship between different zooplankters. The *Cyclops* group is predacious on other zooplankters (Pennak, 1953). On March 1-2, 1959, the populations of *Daphnia galeata mendotae* (a "grazer") and *Cyclops bicuspidatus* (a predator) had similar patterns of distribution (Figures 5 and 22). On August 15-16, and November 22-23, 1958, the populations of *Daphnia galeata mendotae* and of *Mesocyclops edax* have similar patterns of distribution (Figures 3, 4, 20 and 21).

SUMMARY

1. Quantitative vertical series of plankton samples through nine meters of depth were taken at six-hour intervals during a 24-hour period on June 21-22, August 15-16, and November 22-23, 1958, and March 1-2, 1959, in Leavenworth County State Lake, Kansas.
2. Data were obtained for nine species of zooplankters, of which *Daphnia galeata mendotae, Ceriodaphnia lacustris, Diaphanosoma brachyurum, Bosmina longirostris, Diaptomus pallidus, Mesocyclops edax,* and *Chaoborus punctipennis* showed diurnal migration in at least one sampling period. *Chaoborus punctipennis* was the only zooplankter that showed diurnal migration all four sampling times. There was no evidence that any crustacean underwent diurnal migration in November, 1958 or March, 1959.
3. *Mesocyclops edax,* present in June, August, and November, 1958, was replaced in March, 1959, by *Cyclops bicuspidatus.*
4. Light, overturn, size, thermocline, and gravity were important factors that seemed to affect the vertical distribution and migration of the zooplankters; factors of lesser importance were sex, temperature, and oxygen. The daily and seasonal changes in vertical distribution and patterns of migration were probably the result of different combinations of these modifying factors.

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TABLE 1.—Total numbers of liters sampled at all depths, and average number of each species per liter.

Collection		Total liters	Average number of individuals per liter									
Date	Period		*Daphnia galeata mendolae*	*Daphnia pulex*	*Ceriodaphnia lacustris*	*Diaphanosoma brachyurum*	*Bosmina longirostris*	*Diaptomus pallidus*	*Mesocyclops edax*	*Cyclops bicuspidatus*	*Nauplii-metanauplii*	*Chaoborus punctipennis*
June 21–22, 1958	Dawn	1,696	29.4	......	....	0.60	1.56	10.4	18.2	....	96.4	2.60
	Noon	2,792	16.3	......	....	0.03	0.40	8.7	12.0	....	63.1	1.40
	Dusk	2,236	22.7	......	....	0.11	0.20	7.8	14.7	....	88.3	1.40
	Midnight	1,520	31.5	......	....	0.25	0.42	9.9	12.3	....	109.0	10.40
August 15–16, 1958	Dawn	692	8.4	......	22.3	4.20	0.47	29.6	2.4	....	25.2	0.28
	Noon	276	7.6	......	32.5	4.80	0.24	38.8	5.7	....	18.0	0.42
	Dusk	272	8.7	......	25.1	8.50	0.31	51.0	5.7	....	21.9	0.64
	Midnight	152	9.3	......	44.2	9.60	0.62	51.3	2.5	....	23.6	0.54
November 22–23, 1958	Dawn	3,520	14.7	0.9	....	0.40	0.10	10.3	1.7	....	53.7	0.01
	Noon	4,224	16.8	1.3	....	0.22	0.35	11.0	2.1	....	53.9	0.01
	Dusk	2,980	9.4	1.0	....	0.34	0.02	5.8	1.2	....	70.6	0.03
	Midnight	4,044	12.1	0.7	....	0.31	0.19	7.7	1.4	....	57.9	0.04
March 1–2, 1959	Dawn	3,148	7.1	......	....	....	1.70	4.8	....	12.7	45.6	0.00
	Noon	3,492	3.8	......	....	....	1.10	3.1	....	10.0	24.7	0.00
	Dusk	2,806	2.2	......	....	....	0.79	2.0	....	10.0	36.0	0.00
	Midnight	2,758	3.5	......	....	....	0.61	1.8	....	4.6	34.0	0.02

TABLE 2.—Analysis of variance of the transformed counts of 10 one-milliliter samples.

Species	Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Daphnia galeata mendotae	Group means Individuals	3 36	202.2 8.79	67.4 0.244	276.0**
Bosmina longirostris	Group means Individuals	3 36	10.6 5.8	3.0 0.16	21.8**
Diaptomus pallidus	Group means Individuals	3 36	109.4 5.4	12.1 0.15	80.6**
Mesocyclops edax	Group means Individuals	3 36	90.8 29.4	10.0 0.816	12.2**

TABLE 3.—Dissolved oxygen values and temperatures of water in Leavenworth County State Lake, Kansas. Dates when the measurements were made are designated by letters at the head of the columns as follows: J = June 21, 1958; A = August 15, 1958; N = November 19, 1958; M = March 1, 1959.

Depth in meters	Oxygen in mg./1				Temperature in degrees F.			
	J	A	N	M	J	A	N	M
1	10.6	8.0	8.0	11.0	77.4	87.8	52.6	42.2
2	10.6	8.8	7.2	12.4	77.4	87.3	52.3	42.0
3	10.2	9.4	6.8	11.0	77.3	86.8	52.3	41.8
4	9.9	....	....	13.1	77.3	83.6	52.3	41.6
5	....	....	7.2	....	75.5	79.2	52.1	41.2
6	4.8	0.2	8.2	....	67.6	76.2	52.1	41.2
7	5.0	0.4	8.2	14.0	59.0	74.3	52.1	41.2
8	2.5	0.4	7.6	12.1	54.1	69.8	52.1	41.1
9	1.2	0.2	8.0	13.0	51.6	60.2	52.1	41.1

TABLE 4.—Factors that may have modified the vertical distribution and migration of each of nine species of zooplankters in Leavenworth County State Lake, Kansas. Dates when the factors may have been modifiers are designated by letters at the head of the columns as follows: J = June 21-22, 1958; A = August 15-16, 1958; N = November 22-23, 1958; M = March 1-2, 1959.

Species	Light				Temperature				Gravity				Overturn				Thermocline				Oxygen				Size				Sex			
	J	A	N	M	J	A	N	M	J	A	N	M	J	A	N	M	J	A	N	M	J	A	N	M	J	A	N	M	J	A	N	M
Daphnia galeata mendotae	X	X		X		X						X			X	X						X					X					
Daphnia pulex															X																	
Ceriodaphnia lacustris		X								X								X				X										
Diaphanosoma brachyurum	X	X							X	X					X		X	X				X										
Bosmina longirostris	X	X				X				X		X			X	X	X	X									X	X				
Diaptomus pallidus	X	X	X									X			X	X	X					X				X		X	X			
Mesocyclops edax	X	X							X		X				X		X	X				X										
Cyclops biscuspidatus												X				X												X				
Nauplii-metanauplii of Copepoda		X													X	X	X	X				X			X	X	X	X				
Chaoborus punctipennis	X	X	X	X													X	X							X	X	X	X				

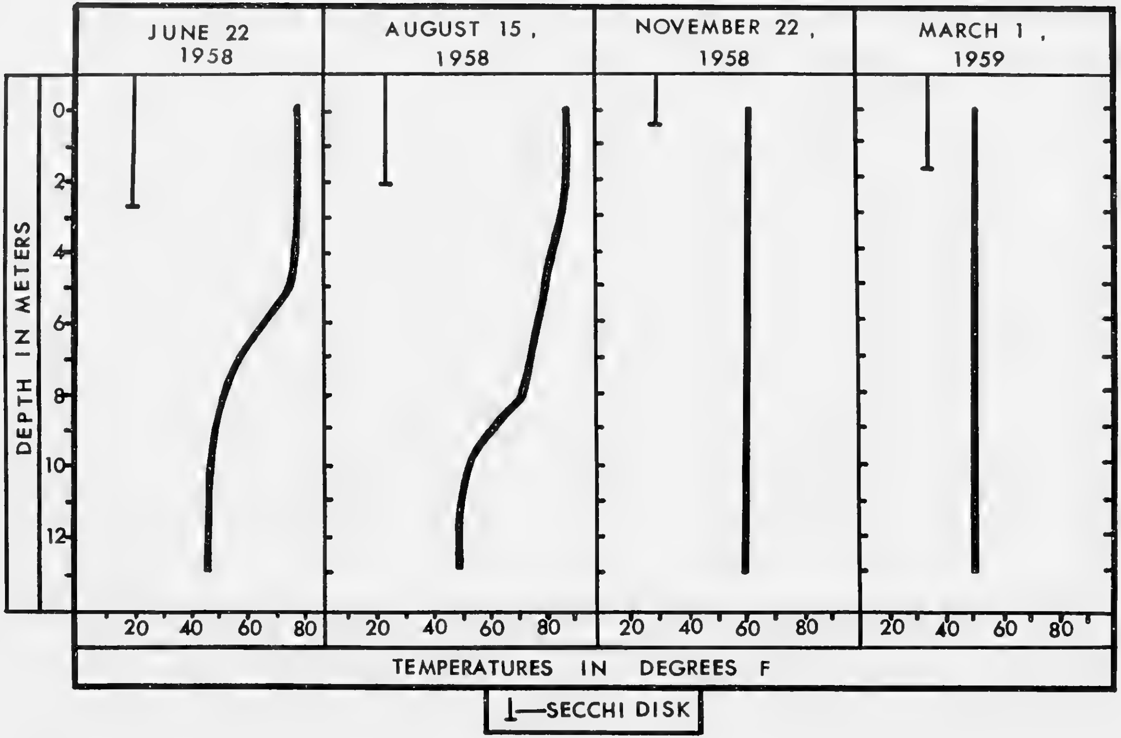
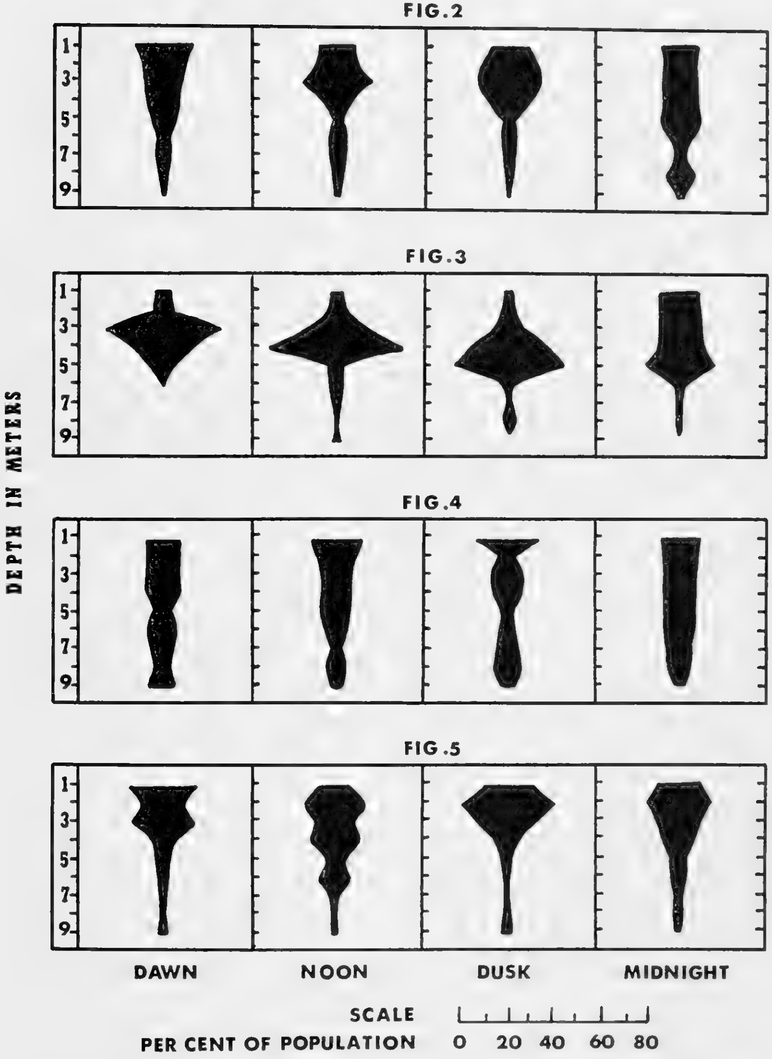


FIG.1

FIG. 1. The graph shows the temperatures in degrees fahrenheit through the first thirteen meters in Leavenworth County State Lake on June 22, August 15, and November 22, 1958, and March 1, 1959. The depth of the Secchi-disk reading on each date is illustrated in the top left corner of each graph.



FIGS. 2-5. Diurnal changes in the vertical distribution of *Daphnia galeata mendotae:* fig. 2: June 21-22, 1958; fig. 3: August 15-16, 1958; fig. 4: November 22-23, 1958; fig. 5: March 1-2, 1959.

FIG. 6

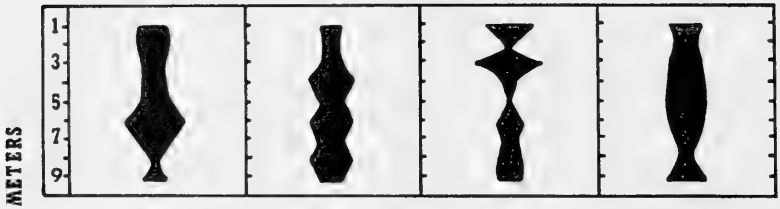


FIG. 7

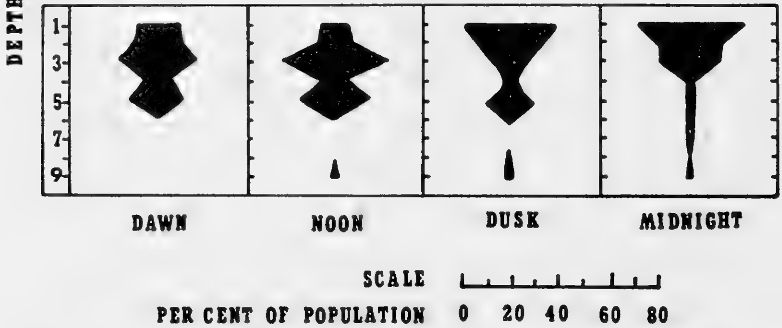
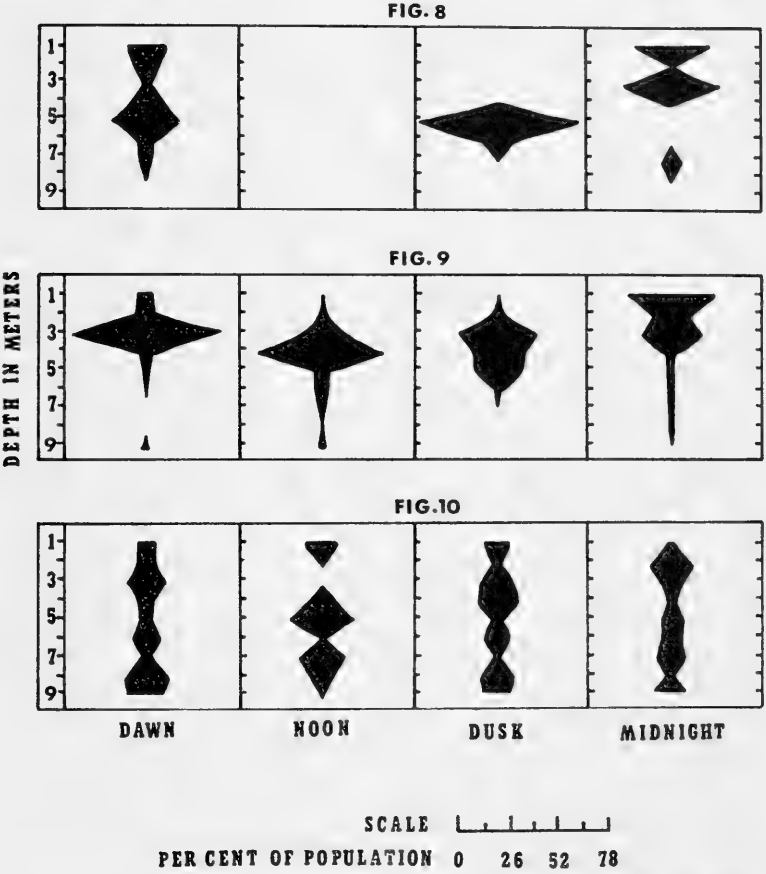
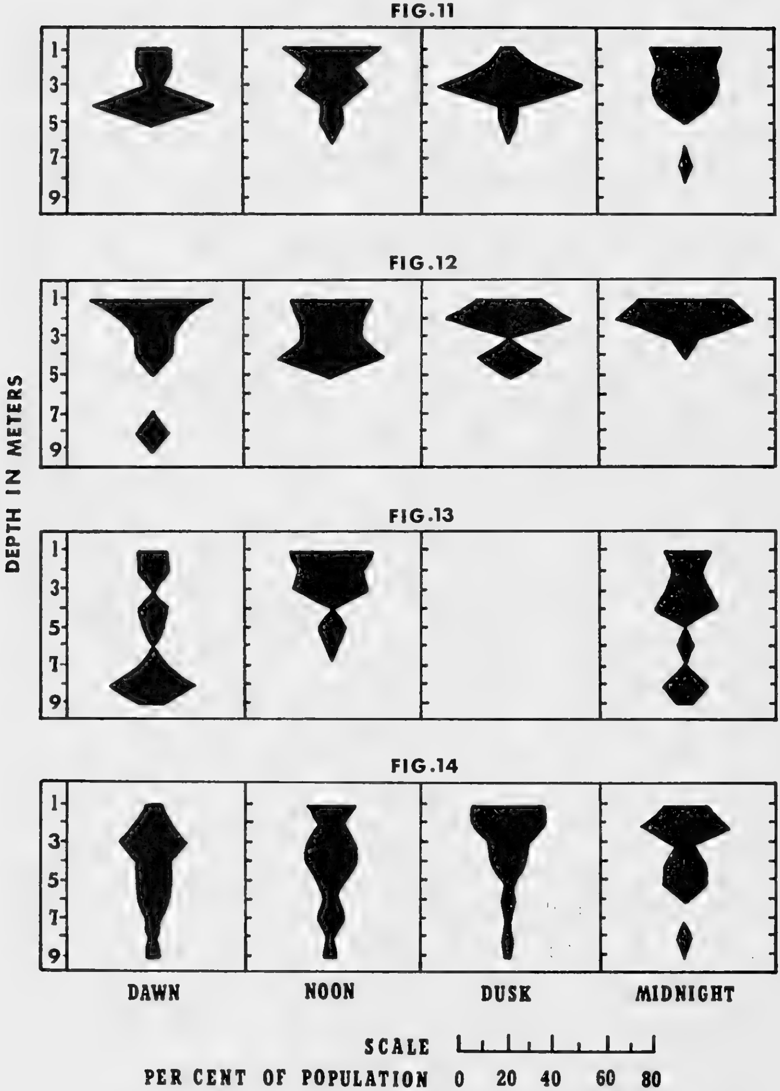


FIG. 6. Diurnal changes in the vertical distribution of *Daphnia pulex* on November 22-23, 1958.

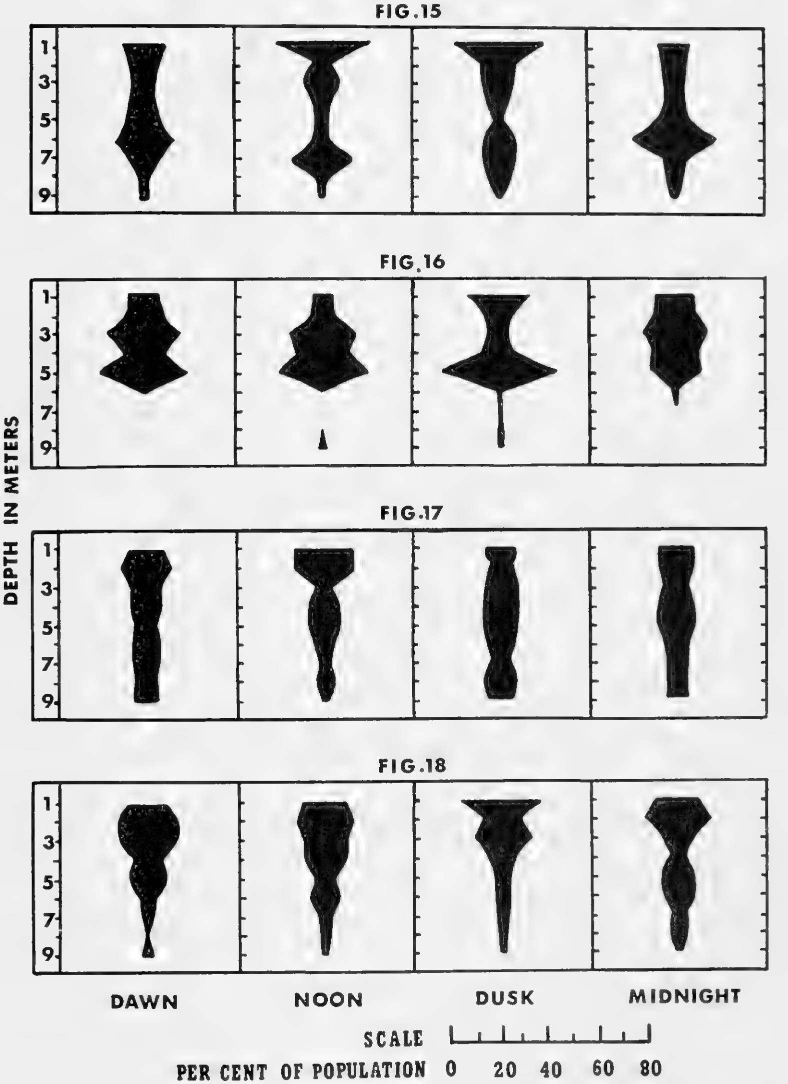
FIG. 7. Diurnal changes in the vertical distribution of *Ceriodaphnia locustris* on August 15-16, 1958.



FIGS. 8-10. Diurnal changes in the vertical distribution of *Diaphanosoma brachyurum:* fig. 8: June 21-22, 1958; fig. 9: August 15-16, 1958; fig. 10: November 22-23, 1958.



Figs. 11-14. Diurnal changes in the vertical distribution of *Bosmina longirostris:* fig. 11: June 21-22, 1958; fig. 12: August 15-16, 1958; fig. 13: November 22-23, 1958; fig. 14: March 1-2, 1959.



Figs. 15-18. Diurnal changes in the vertical distribution of *Diaptomus pallidus:* fig. 15: June 21-22, 1958; fig. 16: August 15-16, 1958; fig. 17: November 22-23, 1958; fig. 18: March 1-2, 1959.

FIG.19

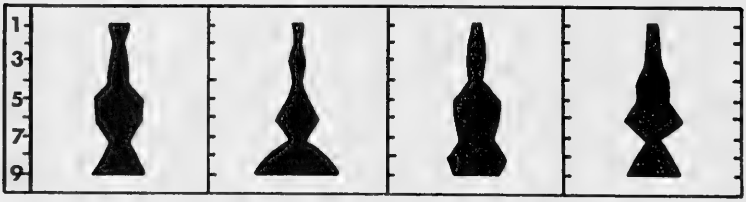


FIG.20

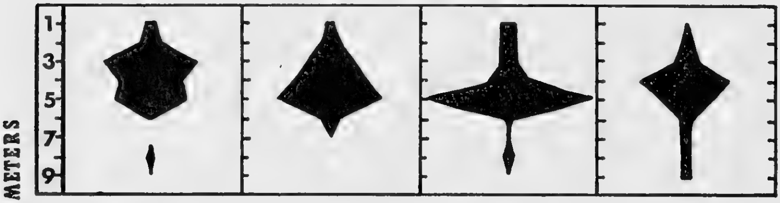


FIG.21

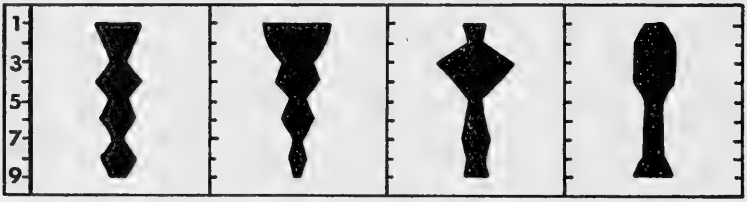
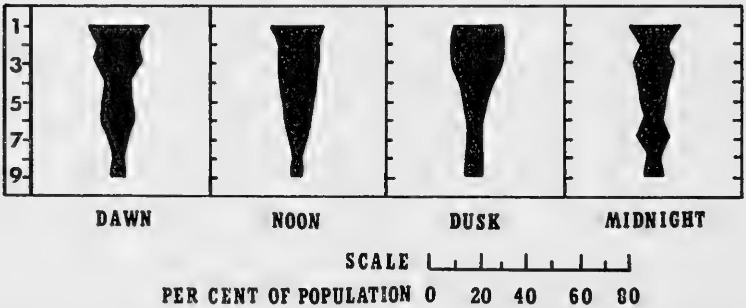
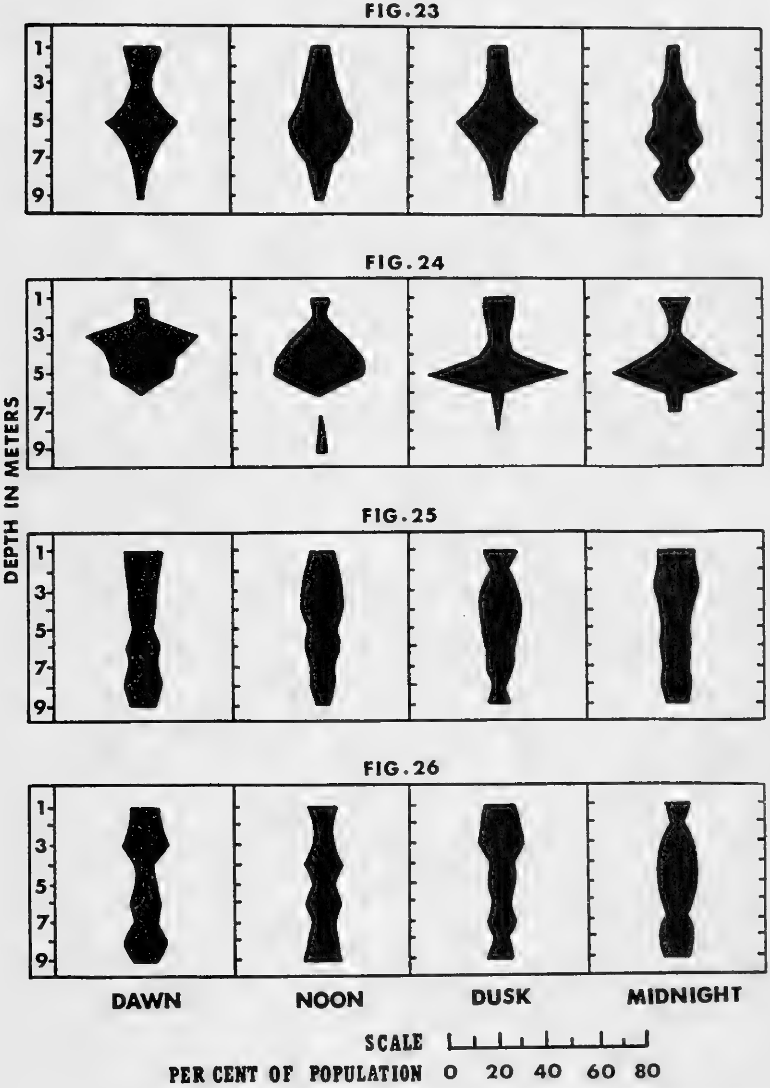


FIG.22

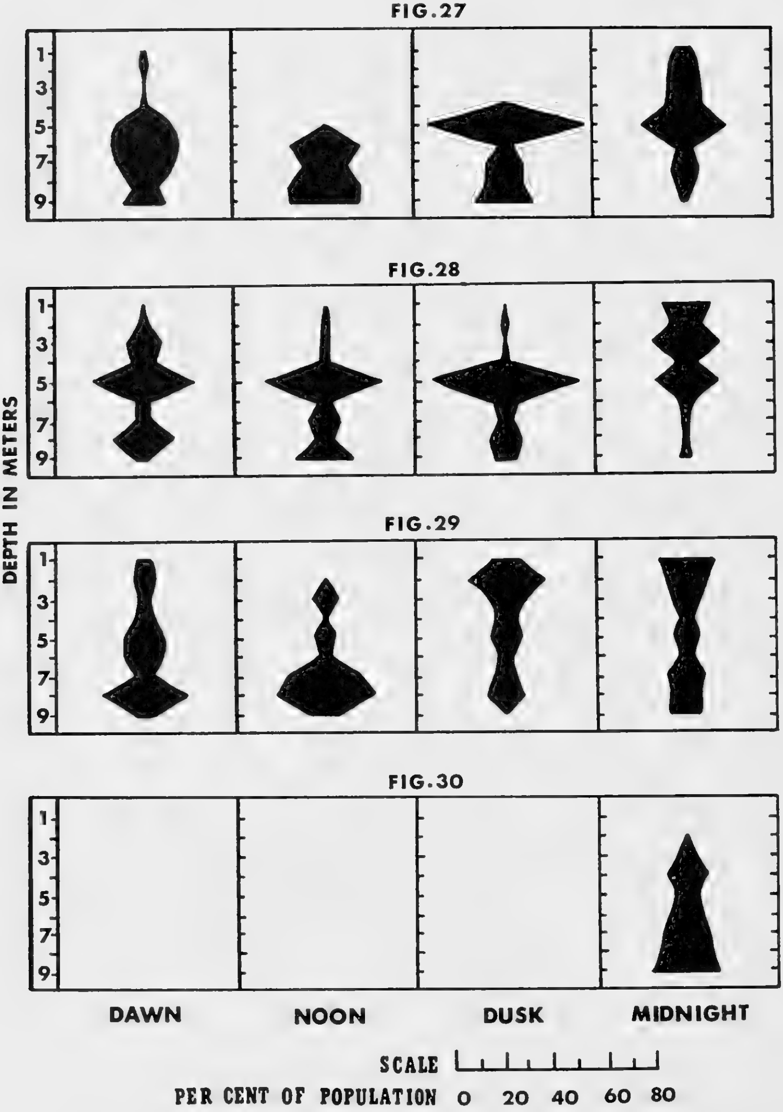


FIGS. 19-21. Diurnal changes in the vertical distribution of *Mesocyclops edax:* fig. 19: June 21-22, 1958; fig. 20: August 15-16, 1958; fig. 21: November 22-23, 1958.

FIG. 22. Diurnal changes in the vertical distribution of *Cyclops bicuspidatus* on March 1-2, 1959.



FIGS. 23-26. Diurnal changes in the vertical distribution of *Nauplii-metanauplii of Copepoda:* fig. 23: June 21-22, 1958; fig. 24: August 15-16, 1958; fig. 25: November 22-23, 1958; fig. 26: March 1-2, 1959.



FIGS. 27-30. Diurnal changes in the vertical distribution of *Chaoborus punctipennis*: fig. 27: June 21-22, 1958; fig. 28: August 15-16, 1958; fig. 29: November 22-23, 1958; fig. 30: March 1-2, 1959.

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The Genus Penstemon in New Mexico[1]

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Abstract: This study is a taxonomic treatment of the 33 species of *Penstemon* known to occur in New Mexico. Synonymy, description, distribution, and ecology are given for each of the taxa represented in the state. Chromosome numbers of 24 species are reported for the first time, and previous counts of four other species have been verified. One large hybrid population of *P. ambiguus* × *P. thurberi* is analyzed and discussed.

INTRODUCTION

In 1938, when this study was first begun, the need for a taxonomic treatment of the genus *Penstemon* in New Mexico was apparent. In the *Flora of New Mexico,* Wooten and Standley (1915) listed the species then known for the state. However, their treatment of the genus was inadequate because of the lack of complete descriptions, errors in recognition of species, errors in nomenclature, inclusion of non-New Mexican species, and omission of several species that do occur in the state. Furthermore, this publication has been out of print for many years.

A Flora of Arizona and New Mexico by Tidestrom and Kettell (1941) is unsatisfactory in its treatment of *Penstemon* although it does contain descriptions of some New Mexican species. Pennell's (1920) *Scrophulariaceae of the Central Rocky Mountain States* is applicable only in northern New Mexico. Studies in *Penstemon* by Keck (1937a, b, 1938, 1945) contain excellent treatments of most of the New Mexican species that belong in the sections discussed in these papers.

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[1] The authors are indebted to a number of people for assistance during the preparation of this study. Dr. E. F. Castetter suggested the original study, encouraged the preparation of this paper, and aided with many personal collections. Special gratitude is due to Dr. David D. Keck without whose valued assistance and co-operation the original study could not have been made. We wish to thank the following for aid in obtaining fresh material or for loan and donation of specimens: Mr. Cleon Mankin, Dr. David D. Keck, Dr. Omar E. Sperry, Dr. A. L. Hershey, and Dr. Lora Shields. Finally we wish to thank Mrs. Fern L. Sweeney for her careful typing and proofreading.

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The present study of *Penstemon* is a continuation of one by Nisbet (1942). The purpose of continued investigation has been to obtain additional information on the distribution, ecology, taxonomy, and cytology of *Penstemon* in New Mexico.

Of the 225 or more species of *Penstemon* in North America, 33 are known to occur in New Mexico. Although the genus is of little economic importance, some species are grazed extensively by cattle. Increased use is being made of the more attractive species as ornamentals, and every year new varieties are being offered to the gardening public by nurserymen.

The penstemons included in this study are limited to those occurring in New Mexico. Therefore, no special attempt has been made to show phylogenetic relationships other than to arrange closely related species into natural groupings.

Thorough and systematic field work must be the basis of any satisfactory taxonomic study since it gives a type of familiarity with the species that cannot be gained in the herbarium. Extensive collections for this study have been made over most of the state. All except four of the species and subspecies listed have been observed and studied in the field in New Mexico, or in a few instances, in adjacent Arizona. Moreover, 28 of these have been grown and studied in the garden.

Penstemon shows great diversity in shape, size, and color of the corollas; in shape, size, and texture of the leaves; in modes of growth; and in habitats. However, members of the genus are easily recognized by the uniformity of the capsules and seeds and by the structure of the sterile stamen. Notwithstanding the diversity of characters that occur in the genus, it is often difficult to distinguish closely related species from one another or to recognize aberrant forms that occasionally occur. Because of these difficulties, steps in the accompanying key often contain more than one set of contrasting characters. In addition, a detailed description is given for each species, subspecies, and variety. Line drawings are given for many of the species in order to help visualize contrasting and outstanding characters and thus aid in the differentiation of species and subspecies. The included photographs show types of inflorescence as well as the general nature of the habitats in which various species are found.

Collection data follow each description. The majority of specimens cited were collected in New Mexico, but some are from adjoining states. Geographical range, blooming period, and type of habitat are given in a general discussion that follows the collection data. While penstemons are either spring or summer flowering, some plants bloom later than usual due to unfavorable moisture conditions or to grazing of the original flower shoots.

Chromosome numbers have been determined for many of the New Mexican species of *Penstemon,* and these indicate an apparent lack of polyploidy of the entities in the area studied. One large putative hybrid population, *P. ambiguus* × *P. thurberi,* has been analyzed by using Anderson's well-known pictorialized scatter diagram method coupled with pollen fertility studies.

METHODS AND MATERIALS

New Mexico is a large state with many rough mountainous areas, parts of which are practically inaccessible. Therefore, much field work remains to be done before it can be said that collections of *Penstemon* for the state are entirely adequate. Nevertheless, extensive field work and careful examination of fresh specimens have made this study possible. Habit, corolla shape, anthers, and staminode were sketched in the field. Field notes on distribution, frequency, type of habitat, and variations in size and shape of the corollas were exceedingly valuable. Large numbers of fresh corollas were measured to ascertain the range in corolla size of certain species. Some colonies of plants were observed two or three years in succession to determine the constancy of stem length, leaf size, flower color, and the number of corollas borne by each peduncle. It was not possible to make such exhaustive studies of all species, but emphasis was placed on those entities of questionable taxonomic status.

Mass collections were made and studied for all New Mexican species and subspecies except *P. bridgesii, P. lanceolatus, P. buckleyi, P. linarioides* ssp. *maguirei,* and *P. pulchellus.* Two plants of *P. bridgesii* from Arizona were studied in the garden during two growing seasons. In studying mass collections, constancies and variations of characteristics were tabulated and the results used in writing the descriptions.

Examination of type specimens was not possible, but isotypes of a few of the species were studied. Original descriptions were analyzed, and careful studies were made of previously published descriptions of those species under consideration. Collections were made at the type localities or in territory contiguous to that of the type collection for those species first collected in New Mexico. If the type locality was not exactly known, plants were collected in the same type of habitat. In the taxonomic treatment of the species, the type locality is indicated after the publication data for those species first collected in New Mexico. *Penstemon linarioides* ssp. *coloradoensis* and *P. strictus* ssp. *strictiformis* were collected at the type localities in southwestern Colorado. *Penstemon breviculis* was collected in three different places near the type locality in southwestern Colorado. *Penstemon auriberbis* was collected not far south of the type locality in Pueblo County, Colorado. *Penstemon pseudospectabilis* ssp. *connatifolius* was collected on Apache Trail, Maricopa County, Arizona, which is the type locality for this subspecies.

Whenever fresh specimens were not available for study, corollas from dried specimens were boiled in water in order to restore their shape for observation and to facilitate more accurate measurements than are possible when using dried specimens.

The collections of *Penstemon* were studied in the following herbaria: The University of New Mexico, New Mexico College of Agriculture and Mechanic Arts, New Mexico Highlands University, Saint Michael's College, Santa Fe, the U. S. Forest Service Regional Office of Region 3, and The University of Arizona. In addition, specimens were borrowed from the Carnegie Institute of Washington at Stanford University, the Rocky Mountain Herbarium, and Sull Ross Teachers College. Abbreviations used for citing herbaria follow the system proposed by Lanjouw and Stafleu (1956).

The herbarium of the University of New Mexico now contains over 800 sheets of *Penstemon.* At New Mexico A. & M. College a number of sheets from the original Wooten and Standley collections were examined. The collection of the U. S. Forest Service Regional Office and minor collections at national and state parks and monuments located in New Mexico and adjacent areas have yielded much information on distribution, blooming period, and other pertinent data.

Material for cytological study was fixed in a mixture of two parts ethyl alcohol and one part propionic acid. Fixation was for a minimum time of forty-eight hours at room temperature. The microsporocytes or somatic tissues of the inflorescence were stained with propionocarmine prepared according to Sass (1951). Some slides were made permanent by withdrawing the stain with filter paper from one side of the cover glass while introducing Venetian turpentine from the other side.

Pollen grains were stained with five percent cotton blue in Aman's lactophenol and examined approximately twenty-four hours later. Those pollen grains with the cytoplasm stained a uniformly deep blue were considered viable while those that did not stain at all or stained only in spots were considered non-viable. Usually 300 or more pollen grains from each plant were counted for the determination of pollen viability.

CYTOLOGICAL OBSERVATION

Chromosome numbers are known for a number of species of *Penstemon* (Darlington and Wiley, 1955). Apparently the basic number of the genus is $n = 8$. Keck (1945) has compiled chromosome numbers for species belonging to the section *Spermunculus* in which diploid, allopolyploid, and autopolyploid forms occur. The chromosome number of all species reported in this paper is $n = 8$. Of the counts presented here, all except those for *P. barbatus, P. oliganthus, P. ovatus,* and *P. rydbergii* are reported for the first time.

The determination of chromosome number was made in most cases from microsporocyte tissue. However, somatic cells from floral tissue were utilized in a few instances. Meiotic stages found best for counting were first or second metaphase or anaphase. When the cells were properly squashed, first or second telophase could be used.

At diakinesis, the chromosomes of some species were found to have threadlike tips and larger, more darkly stained centric regions (Figs. 8, 11, 16). Usually diakinesis was unsatisfactory for study because of the difficulty encountered in staining the chromosomes at this stage. Heterochromatic segments were found in many species at pachytene, and at mitotic prophase differential staining was noted for the heterochromatic segments. Some species apparently contain a mordant either in the anther or corolla pigments because overstaining usually resulted after the same fixation procedure that was applied to other species.

Collection data and a list of the species of *Penstemon* for which chromosome counts have been obtained may be found in Table 1. Of the species listed there, *P. eatoni* ssp. *exsertus, P. ovatus, P. parryi, P. unilateralis,* and *P. subulatus* do not occur in New Mexico. However, counts for some New Mexican species have been made from collections outside the state as indicated in Table 1. Those species and hybrids marked by an asterisk are represented by voucher specimens in the herbarium of the University of New Mexico. Camera lucida drawings of the chromosomes of most of the species are shown in figures 1-23.

TABLE 1.—Chromosome number and collection data for certain species of *Penstemon.*

Species	Chromosome number	Collection data
*P. alamosensis**	n = 8	*Castetter 8136,* Dog Canyon, Otero Co., May, 1955.
P. alpinus ssp. *brandegeei**	n = 8	*Nisbet 2000,* Springer, Colfax Co., June, 1956.
P. ambiguus ssp. *ambiguus**	n = 8	*Jackson* and *Nisbet 1156,* 5 miles south of Belen, Valencia Co., June 23, 1956.
*P. ambiguus × thurberi**	n = 8	*Jackson* and *Nisbet 1158, 1159,* 20 miles west of Socorro, Socorro Co., June 15, 1956.
P. angustifolius ssp. *caudatus*	n = 8	*Nisbet,* Springer, Colfax Co., May, 1956.
P. barbatus ssp. *torryi*	2n = 16	*Nisbet,* Merino Valley, Colfax Co., May, 1956.
P. crandalli ssp. *glabrescens*	n = 8	*Nisbet,* south of Questa, Taos Co., May 15, 1956.
P. crandallii ssp. *glabrescens* var. *taosensis*	2n = 16	*Nisbet,* south of Questa, Taos Co., May 15, 1956.
P. cardinalis ssp. *cardinalis*	n = 8, 2n = 16	*Nisbet,* garden grown plant from seed collected near Capitan, Lincoln Co., June, 1956.
P. eatonii ssp. *exsertus**	n = 8	*Nisbet, 1124,* Queen Creek Canyon, Gila Co., Arizona, March 17, 1957.
P. jamesii	n = 8	*Jackson,* near Cedro, Route 10, Bernalillo Co., May, 1958.
P. linarioides ssp. *coloradoensis**	n = 8	*Jackson* and *Nisbet 1136,* 3 miles north of Mancos, Montezuma Co., Colorado, June 29, 1957.
*P. neomexicanus**	n = 8	*Jackson* and *Nisbet 2019,* 5 miles north of Alto, Lincoln Co., July 22, 1957.
P. oliganthus	n = 8	*Jackson* and *Nisbet 2018,* east of crest, Sandia Mts., Bernalillo Co., July 12, 1956.
P. ovatus	n = 8	*Nisbet,* garden grown, Springer, Colfax Co., May, 1956.
*P parryi**	n = 8	*Nisbet 1149,* near Christmas Mine, Gila Co., Arizona, March 18, 1957.

TABLE 1.—Chromosome number and collection data for certain species of *Penstemon*.—*Concluded.*

Species	Chromosome number	Collection data
*P. pinifolius**	n = 8	*Nisbet 2007*, Pinos Altos, Grant Co., July 8, 1956.
P. pseudospectabilis ssp. *connatifolius*	n = 8	*Nisbet*, 5 miles west of Miami, Gila Co., Arizona, May, 1957.
*P. rydbergii**	n = 8	*Nisbet 2007*, Merino Valley, Colfax Co., June 21, 1955.
P. secundiflorus	n = 8	*Nisbet*, San Miguel Co., May, 1956.
P. strictus	n = 8	*Nisbet*, Merino Valley, Colfax Co., May, 1956.
*P. subulatus**	n = 8	*Nisbet 1151*, east of Superior, Maricopa Co., Arizona, March 17, 1957.
*P. superbus**	n = 8	*Nisbet 1147*, Gila River, Gila Co., Arizona, May 5, 1957.
*P. thurberi**	n = 8	*Jackson* and *Nisbet 1155*, Gage, Luna Co., June 23, 1956.
*P. unilateralis**	n = 8	*Nisbet 2001*, Teller Co., Colorado, July 8, 1956.
*P. virgatus**	n = 8	*Nisbet 2004*, U. S. Hill, Taos Co., July 7, 1956.
*P. whippleanus**	n = 8	*Jackson* and *Nisbet 2002*, Sandia Mts., Bernalillo Co., July 12, 1956.

ANALYSIS OF NATURAL HYBRIDS BETWEEN *PENSTEMON AMBIGUUS* AND *P. THURBERI*

During a field study of *Penstemon ambiguus* and *P. thurberi* in 1939, one of the authors (Nisbet) located a large population of about 5,000 plants near Magdalena, Socorro County, New Mexico, which contained some individuals in the population that seemed to fit the description of *P. thurberi* while others could be keyed to *P. ambiguus.* However, none of the plants completely "fitted" either species, and a great many were intermediate for various characteristics. On the basis of morphological studies, these plants were determined as putative hybrids between *P. ambiguus* and *P. thurberi.*

Both *Penstemon ambiguus* and *P. thurberi* are shrubby species occurring in sandy soils of the southwestern United States. At one time both species were segregated from *Penstemon* and placed in the genus *Leiostemon.* However, more recent authors have retained both species in the section *Ambigui* of *Penstemon.* The ranges of the two species overlap in New Mexico in Socorro, Grant, and Catron counties. The large hybrid swarm found in Socorro County is in an area that has been and still is heavily over-grazed. Hybrids have entirely disappeared from the range area and are now found only along the highway right-of-way where they are protected from cattle by a fence. Neither of the parental species occur in the vicinity of the hybrid populations at the present time. In 1956 this hybrid population was again examined and a mass collection was taken for later study. Mass collections were also made of *P. thurberi* and *P. ambiguus* from different localities. Measurements and observations were made on plants of both species in order to determine the constancy of key characteristics. The same kinds of measurements and observations were made on the mass collection of putative hybrids from near Magdalena.

The variation of morphological characters of the species and hybrids has been shown by use of Anderson's (1946) method of pictorialized scatter diagrams, a method that depicts variations of several characteristics for an individual plant. Pictorialized scatter diagrams of the two species are shown in figure 24. As indicated in the scatter diagram, the species are distinct, especially in flower color, shape of the corolla tube, and size of the corolla. In addition, there is a difference in throat pubescence. Generally there is no overlapping of characteristics, but occasionally one finds a plant of either *P. thurberi* or *P. ambiguus* in which there is some overlap in the length of the coralla lip.

In the hybrid swarm (Fig. 25) individuals with various stages of intermediacy were found. Some of these approached *P. thurberi* very closely, differing only slightly in lobe length and pubescence. Although a number of plants were found to have the *ambiguus*-like corolla, they showed the effects of *thurberi* in having shorter lobes and intermediate pubescence. The corolla face of *P. ambiguus* is white (W) while that of *P. thurberi* is reddish purple (RP). Two intermediate color classes may be distinguished in the putative hybrids. These are pink (P) and pinkish-purple (PP) as indicated in figure 25. From observation of the pictorialized scatter diagram of the hybrids, one can see that some individuals differ from plants of the parental population by only one of the measured characteristics.

The percentage of stainable pollen in plants of the two species and putative hybrids was used as an index of male sterility. This is a common method for obtaining an index of sterility, but it may be subject to some error inasmuch as all normal-appearing pollen grains may not function properly. However, when the parental species and hybrids are compared, one may obtain some idea of the relative fertility of the hybrids.

Pollen fertility was determined for 29 of the hybrids and nine parental plants. The results are listed in Table 2.

TABLE 2.—Percentage of stainable pollen in *Penstemon ambiguus*, *P. thurberi*, and the putative hybrids between the two entities.

Species and hybrids	Number of plants	Percentage range of stainable pollen
P. ambiguus	5	95–100
P. thurberi	4	95–100
P. ambiguus × *thurberi*	15	95–100
	2	82
	1	76
	1	59

The chromosome number of both *P. thurberi* and *P. ambiguus* is $n = 8$. Cytological studies of meioses in several putative hybrids revealed no irregularities, but in some plants reduced pollen viability was evident. However, the majority of the hybrids were highly fertile, having the same range of stainable pollen as found in the parents.

The effects of the hybrid population on the variability of both parental species appears to be negative. Probably the distance separating the parental species and this large hybrid swarm precludes gene flow between the parents and the hybrids. Thus introgression between the species may not occur. However, the presence of a large hybrid population such as the one described here may prove interesting for future study. It is, in effect, a large and highly variable gene pool.

Introgression may be expected to occur, however, if the hybrids and parental species should come together. The chances of this seem small in view of the fact that both species and hybrids are grazed by cattle, and the migration of species or hybrids would be limited to disturbed roadside routes across areas of unsuitable habitats.

TAXONOMIC TREATMENT

KEY TO THE PENSTEMONS OF NEW MEXICO

1. Corolla some shade of red; if pink to rose color, the upper stem leaves connate-perfoliate 2

1. Corolla white or some shade of blue or purple; if pink, the upper stem leaves not connate-perfoliate 14

2. Upper stem leaves connate-perfoliate; corolla pink to rose color 3

2. Upper stem leaves sessile or subcordate; corolla some shade of red but not pink to rose 4

3. Corolla throat expanding gradually; staminode glabrous. 1. *P. pseudospectabilis* ssp. *connatifolius*

3. Corolla throat expanding abruptly; staminode bearded. 2. *P. palmeri* ssp. *palmeri*

4. Leaves 1 mm. wide and 10 to 20 mm. long .... 3. *P. pinifolius*

4. Leaves more than 1 mm. wide and more than 20 mm. long 5

5. Corolla constricted at the orifice 6

5. Corolla not constricted at the orifice 7

6. Stem leaves moderately thin, broadly lanceolate, oblong, or lance-ovate, lower ones 10 to 12 cm. long; calyx 3 mm. long. 4. *P. cardinalis* ssp. *cardinalis*

6. Stem leaves moderately thick, ovate or subcordate, lower ones 5 to 6 cm. long; calyx 4 to 6 mm. long .... 5. *P. cardinalis* ssp. *regalis*

7. Anther sacs dehiscent by a short slit across the connective, the free tips remaining closed .... 6. *P. bridgesii*

7. Anther sacs completely or partially dehiscent, the free tips open 8

8. Anther sacs explanate 9

8. Anther sacs not explanate 10

9. Staminode bearded; stem leaves oblong to broadly ovate. 7. *P. superbus*

9. Staminode glabrous; stem leaves lanceolate .... 8. *P. alamosensis*

10. Inflorescence glandular-pubescent .... 9. *P. lanceolatus*

10. Inflorescence glabrous or slightly puberulous 11

11. Corolla not strongly bilabiate, lower lobes short, rounded, usually spreading .... 10. *P. eatonii*

11. Corolla strongly bilabiate, lower lobes long, narrow, reflexed 12

12. Base of lower lobes of corolla bearded with yellow hairs; calyx lobes 6 to 10 mm. long .... 11. *P. barbatus* ssp. *barbatus*

12. Base of lower lobes of corolla glabrous or bearded with a few white or yellowish hairs; calyx lobes less than 6 mm. long 13

13. Anthers glabrous .... 12. *P. barbatus* ssp. *torreyi*

13. Anthers bearded .... 13. *P. barbatus* ssp. *trichander*

14. Foliage glabrous and slightly to heavily glaucous 15

14. Foliage glabrous or puberulous, not glaucous 18

15. Most of the bracts prominent; inflorescence compact, not secund, the very short pedicels and peduncles giving the effect of a spike of flowers 16
15. Only the lower bracts prominent; inflorescence not spike-like, either somewhat compact and secund or open and not secund 17
16. Bracts broadly ovate, subcordate, mucronate, usually obtuse, retuse, or occasionally acute; corolla pale lavender-blue; tip of staminode sparsely bearded with yellowish hairs . . . . 14. *P. buckleyi*
16. Bracts lance-ovate or ovate, caudate or rarely acuminate; corolla sky-blue, violet-blue, or pink; staminode bearded with deep yellow hairs for fully half its length . . . . 15. *P. angustifolius* ssp. *caudatus*
17. Bracts lanceolate; inflorescence somewhat compact, secund; corolla throat gradually expanded, bearded at base of lower lobes. 16. *P. secundiflorus*
17. Bracts broadly ovate with a short, abruptly pointed tip; inflorescence open and not secund; corolla throat narrow and often somewhat curved, expanded only at the orifice, glabrous at base of lower lobes. 17. *P. fendleri*
18. Leaves mostly linear, less than 35 mm. long 19
18. Leaves lanceolate or wider, or if linear, much more than 35 mm. long 28
19. Staminode glabrous; stems much branched above the base; corolla throat not 2-ridged ventrally 20
19. Staminode bearded; stems not branched except at or near the base; corolla throat 2-ridged ventrally 24
20. Corolla pink externally, white on face of lobes 21
20. Corolla blue, blue-purple, or red-purple 23
21. Corolla 15 to 24 mm. long, throat narrow and curved, upper lobes reflexed, lower lobes projecting 22
21. Corolla 12 to 15 mm. long, throat narrow and somewhat curved or gradually expanded, upper lobes reflexed or spreading, lower lobes projecting or spreading . . . . 19. *P. ambiguus* × *thurberi*
22. Stems puberulous . . . . 18. *P. ambiguus* ssp. *ambiguus*
22. Stems glabrous . . . . 20. *P. ambiguus* ssp. *laevissimus*
23. Corolla 10 to 14 mm. long, throat gradually expanded, all lobes spreading . . . . 21. *P. thurberi*
23. Corolla 12 to 15 mm. long, throat narrow and somewhat curved or gradually expanded, upper lobes reflexed or spreading, lower lobes projecting or spreading . . . . 19. *P. ambiguus* × *thurberi*
24. Stems and leaves puberulous with flat scalelike hairs; leaves scattered on flowering stems; bracts much reduced in size; calyx lobes acute or very short acuminate, scarious margined almost to the tip 25
24. Stems and leaves puberulous with fine erect or retrorse hairs, or leaves glabrous; leaves numerous on flowering stems; bracts not reduced in size; calyx lobes long acuminate, scarious margined only at the base . . 27
25. Stems mostly erect, several; corolla strongly bearded at base of lower lobes; staminode bearded most of its length with golden hairs 26

25. Stems ascending or decumbent, numerous; corolla lightly bearded at base of lower lobes; staminode strongly bearded at tip with golden hairs and behind the tip with white or yellowish hairs. 24. *P. linarioides* ssp. *coloradoensis*

26. Leaves mostly linear .... 22. *P. linarioides* ssp. *linarioides*

26. Leaves mostly oblanceolate .... 23. *P. linarioides* ssp. *maguirei*

27. Leaves glabrous ventrally ...... 25. *P. crandallii* ssp. *glabrescens*

27. Leaves puberulous with fine erect or retrorse hairs. 26. *P. crandallii* ssp. *glabrescens* var. *taosensis*

28. Inflorescence glandular-pubescent 29

28. Inflorescence glabrous or puberulous 38

29. Fascicles of small, obscurely toothed leaves in axils of stem leaves. 28. *P. pulchellus*

29. No fasciculate leaves 30

30. Anther sacs explanate 31

30. Anther sacs not explanate 35

31. Corolla dull purple, lower lobes projecting, 3 to 5 mm. longer than upper lobes .... 27. *P. whippleanus*

31. Corolla white, pale lavender, violet-blue, blue-purple, lower lobes not projecting, not noticeably longer than upper lobes 32

32. Corolla not bearded at base of lower lobes; staminode sparsely bearded at the tip .... 32. *P. albidus*

32. Corolla bearded at base of lower lobes; staminode conspicuously bearded 33

33. Corolla 5 to 6 mm. wide, orifice as high or higher than wide; lower lip not glandular within; staminode not or barely exserted. 31. *P. breviculus*

33. Corolla 8 to 15 mm. wide, orifice much wider than high; lower lip glandular within; staminode prominently exserted 34

34. Corolla 25 to 35 mm. long, 10 to 15 mm. wide. 29. *P. jamesii* ssp. *jamesii*

34. Corolla 17 to 22 mm. long, 8 to 10 mm. wide. 30. *P. jamesii* ssp. *ophianthus*

35. Staminode glabrous .... 33. *P. dasyphyllus*

35. Staminode bearded 36

36. Leaves finely toothed .... 34. *P. gracilis*

36. Leaves entire or undulate 37

37. Median stem leaves shorter than internodes; bracts much reduced; lower lobes of corolla longer than upper .... 35. *P. oliganthus*

37. Median stem leaves longer than internodes; bracts not much reduced; upper and lower lobes of corolla subequal .... 36. *P. auriberbis*

38. Inflorescence not at all secund, corollas in dense fascicles usually separated by long internodes, corolla 10 to 14 mm. long. 37. *P. rydbergii*

38. Inflorescence more or less secund, corollas not in dense fascicles, or if so, the fascicles not separated by long internodes, corolla 15 to 40 mm. long 39

39. Leaves lance-ovate or oblong; inflorescence usually broad and compact; corolla 30 to 40 mm. long ..... 38. *P. alpinus* ssp. *brandegeei*
39. Leaves linear or lanceolate; inflorescence usually narrow and elongated; corolla 15 to 30 mm., occasionally 35 mm. long 40
40. Anthers villous 41
40. Anthers glabrous 42
41. Calyx lobes 3 to 6 mm. long; corolla throat moderately inflated above and below; staminode glabrous or with a few short hairs at the tip. 39. *P. strictus* ssp. *strictus*
41. Calyx lobes 8 to 10 mm. long; corolla throat ventricose below, not inflated above; staminode more or less bearded. 40. *P. strictus* ssp. *strictiformis*
42. Corolla 15 to 24 mm. long, 7 to 10 mm. wide, glabrous or lightly bearded at base of lower lobes; staminode narrow or somewhat dilated; stems puberulous or glabrate .... 41. *P. virgatus*
42. Corolla 25 to 35 mm. long, 10 to 17 mm. wide, usually strongly bearded at base of lower lobes; staminode much dilated and often notched at the tip; stems glabrous .... 42. *P. neomexicanus*

1. *Penstemon pseudospectabilis* ssp. *connatifolius* (A. Nels.) Keck, Amer. Midl. Nat. 18:807. 1937.

Penstemon spectabilis Woot. and Standl., not of Thurb., Contr. U. S. Nat. Herb. 19:583. 1915.
Penstemon connatifolius A. Nels., Amer. Jour. Bot. 18:437. 1931.

Stems 4 to 10 dm. tall, several to many from a woody base, glabrous; leaves relatively thin, slightly glaucous or bright green, serrate with somewhat coarse or fine pungent teeth or almost entire; basal and lower stem leaves petiolate, lance-ovate to broadly ovate; median stem leaves sessile or nearly so, upper stem leaves connate-perfoliate and forming disks up to 18 cm. long and 7.5 cm. broad; inflorescence often half the height of the plant, peduncles and pedicels glabrous, lower ones often elongated; calyx 5 to 7 mm. long, glabrous, lobes ovate to elliptic, acute or more often acuminate, narrowly scarious margined; corolla pale to deep rose or rose-magenta, with darker guide lines, 22 to 33 mm. long, up to 12 mm. wide when pressed, glandular without and within, obscurely bilabiate, the throat gradually widening; anther sacs explanate, as broad as long; staminode included, narrow or somewhat dilated, glabrous. Figures 29-31.

Specimens examined: ARIZONA. *Gila County:* Apache Trail, April 6, 1957, *Nisbet 1129* (UNM). *Graham County:* Graham Mountains, March 13, 1936, *U. S. Dept. Agr.* (UNM). *Greenlee County:* 19 miles north of Clifton, June 1, 1940, *Turner* and *Nisbet 801* (UNM). *Pinal County:* Oracle, April 4, 1940, *Turner* and

Nisbet 711 (UNM). NEW MEXICO. *Catron County:* Reserve to Glenwood, June 8, 1950, *Castetter 5859* (UNM); White Water Creek, May 30, 1939, *Nisbet 48* (UNM). *Dona Ana County:* Dripping Springs, Organ Mountains, May 24, 1952, *Castetter 5860* (UNM). *Grant County:* Mule Creek Pass, May 21, 1940, *Turner* and *Nisbet 813* (UNM). *Hidalgo County:* Coronado Forest, May 12, 1945, *Hershey 3538* (UNM).

The specimens from New Mexico designated as *P. spectabilis* by Wooton and Standley are *P. pseudospectabilis* ssp. *connatifolius, Penstemon spectabilis* Thurb. being confined to southern California and Baja California. Subspecies *connatifolius,* the eastern form of *P. pseudospectabilis* Jones, occurs in west central, central, and southeastern Arizona and in southwestern New Mexico. Subspecies *connatifolius* is distinguished from ssp. *pseudospectabilis* by a lack of glands on the pedicels and calyces and by greener and thinner leaves. However, some plants from near Reserve, Catron County, have leaves which are thicker than those typical for this subspecies.

Subspecies *connatifolius* is one of the more beautiful penstemons and well worthy of garden cultivation. If conditions are favorable, it is a long-lived perennial that can be easily grown from seed. Like many other penstemons, this subspecies grows in rocky washes and on gravelly slopes in pinon-juniper-oak woodlands and in yellow pine forests. Plants of this subspecies bloom in April and May at lower altitudes and into June at higher elevations.

2. *Penstemons palmeri* A. Gray, Proc. Amer. Acad. Arts and Sci., 7:379. 1868.

Stems stout, erect, few to several, glabrous or puberulous, 5 to 18 dm. tall; leaves green or glaucous, often grayish, irregularly dentate with pungent teeth or the upper stem leaves subentire, basal and lower stem leaves lanceolate or lance-ovate, petiolate, median stem leaves sessile or clasping, upper stem leaves and lowermost bracts connate-perfoliate, largest to 24 cm. long and 9 cm. wide; inflorescence strict, secund, glandular-pubescent, often over half the height of the plant, peduncles with two to four flowers, bracts very small except the lowermost; calyx 4 to 6 mm. long, lobes ovate, acute, margins scarious; corolla 25 to 35 mm. long, 12 to 22 mm. wide, white, pale pink, or rose-pink, with reddish guide lines, tube short, throat abruptly and widely expanded, lobes reflexed, the lower ones twice as long as the upper, bearded on lower lip; anthers explanate, twice as long as wide, the upper pair of fertile stamens glandular-puberulous near the base; staminode exserted, tip uncinate and strongly bearded with long yellow hairs, base glandular-pubescent.

Specimens examined: ARIZONA. *Coconino County:* Northeast of Prescott, June 8, 1945, *Clark 12723* (UNM). *Mohave County:* May 22, 1938, *Buzon A98* (UNM). *Yavapai County:* 20 miles south of Sedona, July 21, 1935, Whiting *756/1207* (UNM); Mingus Mountain, June 11, 1958, *Nisbet 1185* (UNM); Near Mayer, June 12, 1958, *Nisbet 1188* (UNM). NEW MEXICO. *Torrance County:* 70 miles east of Albuquerque along route 66, June 27, 1959, *Nisbet 2021* (UNM).

Penstemon palmeri is native to central and northwestern Arizona and adjacent sections of Utah, Nevada, and California. A well established colony of this species was found along route 66 about 70 miles east of Albuquerque. This colony is growing at the north end of the Pedernal Hills in pinon-juniper country. At the time these plants were found, June 27, the upper inflorescence contained many buds showing that the blooming period would extend into July. *Penstemon palmeri* is a beautiful penstemon and possesses a delicate fragrance which makes it a welcomed addition to the flora of New Mexico.

3. *Penstemon pinifolius* Greene, Bot. Gaz. 6:218. 1881.

Stems 10 to 45 cm. tall, numerous, forming small mats, woody well above the base, puberulous to almost glabrous; leaves 1 mm. wide or less, 6 to 20 mm. long but occasionally longer, thick, glabrous, crowded on the lower part of the stems, scattered on the upper part; inflorescence secund, the solitary peduncles bearing one or two flowers but sometimes more on vigorous plants; peduncles, pedicels, sepals, and the outside surfaces of the corollas glandular-pubescent; calyx 5 to 7 mm. long, the lobes lanceolate or long acuminate, the margins of the base scarious; corolla 25 to 32 mm. long, scarlet, strongly bilabiate, the narrow two-ridged throat 4 mm. wide when pressed and twice as long as the tube, upper lobes projecting, the long, narrow lower lobes spreading or reflexed, pubescent at the base with long, flat, yellow hairs; anther sacs explanate, longer than wide; staminode included, not dilated, bearded for most of its length with bright yellow hairs. Figures 26-28.

Specimens examined: ARIZONA. *Cochise County:* Chiricahua Mountains, July 7, 1946, *Reed 220* (UNM). *Santa Cruz County:*

Coronado National Forest, July 14, 1938, *Clark 8056* (UNM). NEW MEXICO. *Catron County:* Mogollon Creek, *Metcalfe 2401* (ARIZ); Holt Mountain, *Wooton* (NMC). *Grant County:* Near Pinos Altos, *Stewart* (CI); Cherry Creek, June 18, 1955, *Castetter 8327* (UNM). *Sierra County:* Hillsboro Peak, *Metcalfe 1163* (NMC). *Socorro County:* Hop Canyon, Magdalena Mountains, July 6, 1940, *Nisbet 759* (UNM, CI).

Penstemon pinifolius is not common. It is a summer flowering species that grows in small pockets of soil on rocks and cliffs at high elevations in the mountains of southwestern New Mexico, southeastern Arizona, and adjacent Mexico. In spite of its preference for rocky areas in high mountains, it has been successfully grown in gardens from New England to Oregon.

4. *Penstemon cardinalis* Woot, and Standl. ssp. *cardinalis,* Contr. U. S. Nat. Herb. 16:171. 1913. The type was collected by Wooten on White Mountain Peak immediately above the forks of Ruidoso Creek, July 6, 1895.

Penstemon crassulus. Woot. and Standl., Contr., U. S. Nat. Herb. 16:172. 1913.

Stems 4 to 7 dm. tall, few to several, glabrous, green, or slightly glaucous; leaves moderately thin, glabrous, sometimes mucronate, the basal ones elliptic, spatulate, or ovate, petiolate, mostly obtuse, stem leaves 3 to 12 cm. long, broadly lanceolate, oblong, or lance-ovate, acute, sessile; inflorescence usually secund, narrow, the lower peduncles and pedicels somewhat elongated but erect, bracts very small except the lowest pair; calyx 3 to 3.5 mm. long, lobes ovate, acute or obtuse, margins scarious; corolla 22 to 30 mm. long, dull red or crimson, obscurely bilabiate, the long throat gradually and moderately inflated, constricted at the orifice, lobes 2 to 3 mm. long, upper ones erect, lower ones spreading or reflexed and heavily bearded at the base with long, soft, yellow hairs; stamens included, anther sacs not completely dehiscent, denticulate on the edges; staminode not dilated, bearded at and near the tip. Figures 32, 33, and 36.

Specimens examined: NEW MEXICO. *Lincoln County:* Capitan Pass, Capitan Mountains, July 5, 1940, *Nisbet 747* (UNM, CI); Capitan Mountains, *Hendricks 36103* (U. S. Forest Service Regional Office, Albuquerque, New Mexico). *Otero County:* Sierra Blanca Peak, *Wolf 2871* (CI).

The type of *P. crassulus* differs from the type of *P. cardinalis* only in minor characteristics of leaf and calyx, neither of which is constant over a definite geographical area. Therefore, *P. crassulus* is here considered synonymous with *P. cardinalis*. *Penstemon cardinalis* grows on rocky ridges associated with pine or fir and spruce, blooming from the last of June through July.

5. *Penstemon cardinalis* ssp. *regalis* (A. Nels.) Nisbet and Jackson, comb. nov.

Penstemon regalis A. Nels., Amer. Jour. Bot. 21:578. 1934.

The type was collected by Convis near Carlsbad Caverns in May, 1930.

Leaves moderately thick, firm, the cauline ones 2.5 to 6 cm. long, ovate or subcordate, often obtuse, the lower ones sometimes elliptic; calyx 4 to 6 mm. long, the lobes ovate, acute to acuminate. Figures 34-35.

Specimens examined: NEW MEXICO. *Eddy County:* Guadalupe Mountains, May 12, 1939, *Hershey* and *Nisbet 674* (UNM, NMC); Sitting Bull Falls, May 19, 1951, *Castetter* (UNM); near Carlsbad Caverns, *Convis* 75 (RM).

The differences between *P. cardinalis* ssp. *cardinalis* and ssp. *regalis* are obscure in some specimens. Neither entity has been reported as occurring in the Sacramento Mountains which lie between the White and Guadalupe Mountains. This apparent discontinuous distribution may be the result of insufficient collecting in the southern Sacramento Mountains and the northern end of the Guadalupe Mountains; but based on present information, the ranges of the two entities do not overlap.

Subspecies *cardinalis* and *regalis* show their relationship to *P. havardii* A. Gray in the constricted orifice of the corolla. *Penstemon havardii* occurs to the south in the mountains of Texas; thus it is more closely associated geographically with ssp. *regalis*. However, *P. havardii* differs from the New Mexican species in having the inflorescence glandular-pubescent, corollas nearly scarlet, lobes 5 mm. long, orifice glabrous, staminode glabrous, and anther sacs explanate.

Penstemon cardinalis ssp. *regalis* blooms in May and June in rocky canyons of the pine woodlands.

6. *Penstemon bridgesii* A. Gray, Proc. Amer. Acad. Arts and Sci. 7:379. 1868.

Stems 3 to 6 dm. tall, herbaceous or often woody at the base, glabrous or puberulous below the inflorescence; lower leaves narrowly oblanceolate, upper ones linear, not crowded, glabrous or nearly so; inflorescence narrow, glandular-pubescent, peduncles two- to five-flowered; calyx 4 to 6 mm. long, lobes ovate or lanceolate, acuminate, not scarious margined or only narrowly so on the base; corolla 22 to 27 mm. long, scarlet, strongly bilabiate, throat only slightly inflated, glabrous within, upper lobes projecting, lower ones reflexed; anther sacs partially dehiscent by a short confluent slit leaving the lower portion of each sac closed, edges of the opening minutely denticulate; staminode glabrous, not dilated. Figures 37 and 38.

Specimens examined: ARIZONA. *Yavapai County:* Mogollon Rim, September 2, 1956, *Nisbet 1021* (UNM); 21 miles southeast of Camp Verde, route 79, June 17, 1959, *Nisbet 2023* (KANU). NEW MEXICO. *Catron County:* Trujillo's Ranch on the Frisco (San Francisco) River, 1900, *Wooton* (NMC).

The range of *P. bridgesii* is California to extreme western New Mexico and southern Utah and Nevada to southern Arizona. In spite of this wide range, the plants are few and scattered. *Penstemon bridgesii* was collected in the San Francisco Mountains of Catron County, New Mexico, in 1900, but no recent collections have been reported for the state. The species grows in pockets of soil on rocky cliffs in pinon-juniper or pine woodlands and blooms from June to September. It is easily distinguished from *P. barbatus* by the peculiar dehiscence of the anthers described above.

7. *Penstemon superbus* A. Nels., Proc. Biol. Soc. Wash. 17:100. 1904.

Penstemon puniceus A. Gray, U. S. and Mex. Bound. Bot. Rpt. 113. 1859. Not *P. puniceus* Lilja, 1843.

Stems 3 to 12 dm. tall, one to several, stems and leaves usually strongly glaucous and blackening in drying; basal leaves oblanceolate, spatulate, or elliptic, with margined petioles, stem leaves thickish, broadly ovate, elliptic, or oblong-ovate, acute or barely obtuse, clasping-cordate or slightly connate-perfoliate; inflorescence narrow, often over half the height of the plant, peduncles, pedicels, and calyces with scattered glands or almost glabrous; lowest bracts leaflike, the upper becoming very small; calyx 4 to 5 mm. long, lobes ovate or elliptic, acute or short acuminate, scarious margined; corolla 17 to 22 mm. long, bright orange-pink to scarlet, glandular-pubescent externally and on the lobes, very obscurely bilabiate, almost salverform, throat only slightly expanded, orifice small and circular, lobes broad and flaring; anther sacs included, explanate, as broad as long; staminode included, not dilated, bearded near the tip, hairs sometimes few and short. Figures 39, 40, 42, 44, 82.

Specimens examined: MEXICO. CHIHUAHUA: Benton's Ranch, May 7, 1940, *Hershey 3504* (UNM). ARIZONA. *Cochise County:*

North of Douglas, June 3, 1932, *Clark 4885* (UNM). *Gila County:* Gila River, May 5, 1957, *Nisbet 1147* (UNM). *Greenlee County:* Mule Creek Pass, May 29, 1940, *Turner and Nisbet 803* (UNM). NEW MEXICO. *Grant County:* Mule Creek Pass, March 30, 1940, *Turner* and *Nisbet 708* (UNM). *Hidalgo County:* South of Animas, June 5, 1948, *Dittmer* and *Castetter 5873* (UNM); Cloverdale Canyon, May 14, 1955, *Castetter 7567* (UNM).

Penstemon superbus is truly superb; the tall plants with large glossy leaves and long inflorescence with many brightly colored flowers are very attractive. It flowers from March to June in rocky canyons and along washes in sandy or gravelly soil of the pinon-juniper and oak woodlands or often in the lower yellow pine forests. This species is not common, but its range includes southwestern New Mexico, southeastern Arizona, and the states of Chihuahua and Sonora in Mexico.

8. *Penstemon alamosensis* Pennell and Nisbet, sp. nov.

Caulis 3-7 dm. *altus, tenuis, glaber; folia glabra, glauca, laminis inferioribus magnis ellipticis petiolatis, superioribus parvis lanceolatis sessilibus; thyrsus angustus, minute glanduloso-pubescens, pedunculis bifloris; sepula* 3-5 mm. *longa, ovata lanceolatave, acuta, marginibus scariosis; corolla* 20-25 mm. *longa, rubra; antherae explanatae; filamentum sterile glabrum.*

Stems 3 to 7 dm. tall, slender, solitary or few, glabrous, green, or very slightly glaucous; basal leaves elliptic, obovate, or broadly lanceolate, petiolate, acute to obtuse, stem leaves much reduced in size, two to four pairs, sessile, lanceolate or narrowly oblong, acute; inflorescence narrow, subsecund, usually as much as half the height of the plant, pedicels longer than the peduncles, each peduncle with one to four flowers, two flowers being most common; pedicels, calyces, and the outside of the corollas sparingly glandular-pubescent; calyx 3 to 5 mm. long, lobes ovate to lanceolate, acute or acuminate, narrowly scarious margined; corolla 20 to 25 mm. long, 5 to 7 mm. wide when pressed, bright red, nearly regular, throat gradually and very moderately inflated, lobes spreading; stamens included, anthers explanate; staminode glabrous, not dilated. Figures 41, 43, 45.

The type was collected by G. Nisbet and C. Mankin, June 10, 1941, in a limestone crevice of a dry, rocky wash in Alamo Canyon which is on the west slope of the Sacramento Mountains about five miles southeast of Alamogordo, Otero County, New Mexico. The type specimen (*Nisbet 817*) is in the herbarium of the Academy of Natural Science of Philadelphia. Isotypes have been placed in the herbaria of the Carnegie Institute of Washington and The University of New Mexico.

Specimens examined: NEW MEXICO. *Otero County:* Alamo Canyon, Sacramento Mountains, June 10, 1941, *Nisbet 816* (UNM, CI, PH); Dry Canyon, Sacramento Mountains, northeast of Alamogordo, *Rehn* and *Viereck* (CI); Dog Canyon, 10 miles southeast of Alamogordo, June 5, 1955, *Castetter* and *Nisbet 8136* (UNM).

Penstemon alamosensis, P. wrightii Hook., *P. superbus* A. Nels., and *P. parryi* A. Gray form a group of related species which are characterized by nearly regular corollas with flaring lobes of varying shades of red, explanate anthers, and glabrous or more or less glaucous foliage. *Penstemon wrightii* occurs 175 miles to the southeast of Alamogordo in the Jeff Davis Mountains of Texas. *Penstemon superbus* is found some 200 miles to the west in southwestern New Mexico, while *P. parryi* grows in southern and eastcentral Arizona and does not come into New Mexico. *Penstemon alamosensis* is apparently an endemic restricted to the west slope of the Sacramento Mountains east of Alamogordo.

Penstemon alamosensis is distinguished from *P. superbus* by the characteristics given in the key and in the descriptions of the two species. A careful comparison of fresh specimens indicated that the two species, *P. wrightii* and *P. superbus*, are more closely allied morphologically than either of the two is related to *P. alamosensis*. Garden culture and artificial hybridization of the members of this group might help to determine which should be considered as subspecies. *Penstemon alamosensis* may be distinguished from *P. wrightii* by the following characteristics:

P. alamosensis	*P. wrightii*
Leaves mostly basal; stem leaves reduced in size, two to four pairs, mostly lanceolate and acute, green or slightly glaucous, ratio of length to width, 4:1.	Stem leaves ample and not reduced in size, four to six pairs, ovate or oblong, mostly obtuse, moderately glaucous, ratio of length to width, 2:1.
Lower peduncles seldom more than two-flowered, all bracts very small.	Lower peduncles usually six-flowered, lower bracts leaflike, other small.
Corolla bright red, 20 to 25 mm. long, tube longer than the calyx, throat gradually expanded.	Corolla scarlet, 15 to 20 mm. long, tube no longer than the calyx, the throat abruptly expanded but not widely so.
Staminode glabrous.	Staminode retrorsely bearded on the upper half.

Under favorable conditions *P. parryi* produces many stems which may be 12 dm. or more in height. The stems and leaves are glabrous while the inflorescence is lightly glandular-pubescent. The stem leaves are narrowly to widely lanceolate. The inflorescence is not crowded but each peduncle may be many-flowered. The corollas are 20 to 23 mm. long and deep pink to rose colored. The throat is gradually expanded, the base of the lower lobes are lightly bearded, and the staminode is somewhat dilated and bearded with yellow, retrorse hairs. The narrower leaves and more gradually inflated corollas resemble those of *P. alamosensis.*

Penstemon alamosensis flowers in May and early June on north or northeast facing slopes of rocky limestone ridges, in crevices of the limestone, in dry washes, or at the foot of limestone cliffs. When there is ample winter moisture, the plants are fairly abundant; but the recent drought years have greatly reduced their number. *Penstemon alamosensis* grows only in the lower canyons associated with ocotillo, several species of cacti, agave, yucca, and other semi-desert plants. How far south in the Sacramento Mountains *P. alamosensis* occurs has not been determined, but it has not been found to the north in the White Mountains.

9. *Penstemon lanceolatus* Benth., Pl. Hartw. 22. 1839.
   Penstemon pauciflorus Greene, Bot. Gaz. 6:218. 1881.

Stems 4 to 5 dm. tall, usually densely puberulous with fine hairs but sometimes lightly puberulous; leaves linear, puberulous, often folded on the midrib, about 8 cm. long, apiculate; inflorescence narrow with few flowers, densely glandular-pubescent; calyx about 6 mm. long, lobes ovate or elliptic with narrow scarious margins on the basal portions or not at all scarious; corolla scarlet or dark red, 25 to 30 mm. long, tube short, throat gradually and moderately expanded, glabrous on the lower lobes; anther sacs deep, not explanate but dehiscent from apex to base, denticulate along the edges; staminode included, glabrous, not dilated. Figure 46.

Specimens examined: NEW MEXICO. *Hidalgo County:* Alamo Hueco Mountains, June 21, 1937, *Woods 6-B* (UNM); 6 miles south of Lordsburg, near Banner Mine, June 11, 1960, *McCurdy* & *Nisbet 2023* (KANU).

This species is not at all common. It occurs in rocky canyons of the pinon-juniper or pine woodlands. Its range includes southwestern New Mexico, southeastern Arizona, and the neighboring states of northern Mexico.

10. *Penstemon eatonii* A. Gray, Proc. Amer. Acad. Arts and Sci. 8:395. 1872.

Stems 3 to 6 dm. tall, solitary or few, glabrous or puberulous; stem leaves lanceolate to ovate, clasping to subcordate, acute to acuminate; inflorescence narrow with many flowers, peduncles and pedicels short, bracts small; calyx 4 to 8 mm. long, lobes ovate, acute to acuminate, margins scarious and more or less erose; corolla 20 to 30 mm. long, glistening scarlet, glabrous, obscurely bilabiate, throat only slightly expanded, the lobes about equally erect or spreading; anther sacs dehiscent only part of the length from the free tips, edges denticulate; staminode not dilated, glabrous or with a very few short hairs on the tip. Figure 47.

Specimens examined: ARIZONA. *Coconino County:* Main road, Kayenta Coal Mine, May 29, 1935, *Howell 96* (UNM). *Maricopa County:* Queen Creek Canyon near Superior, March 17, 1957, *Nisbet 1124* (UNM). *Mohave County:* Kingman, April 18, 1957, *Nisbet 1114* (UNM). *Yavapai County:* Apache Trail, April 6, 1957, *Nisbet 1125* (UNM).

No recent collections of *P. eatonii* have been made in New Mexico. A specimen was collected in the Carrizo Mountains west of Shiprock, San Juan County, by Standley prior to 1915. Probably the form that comes into New Mexico is *P. eatonii* ssp. *undosus* (M. E. Jones) Keck in which the stem and leaves are puberulous and the stamens are included or barely exserted. *Penstemon eatonii* flowers from April to July or as early as March in southcentral Arizona. Its range includes southern Utah, the San Juan Valley of southwestern Colorado, much of Arizona, and perhaps the extreme northwestern corner of New Mexico.

11. *Penstemon barbatus* (Cav.) Roth. ssp. *barbatus,* Cat. Bot. 3:49. 1806.

Chelone barbata Cav., Icones Pl. 3:22, 242. 1794.
Penstemon barbatus var. *puberulous* A. Gray, U. S. and Mex. Bound. Bot. Rpt. 114. 1859.

Stems 3 to 18 dm. tall, solitary to several, usually stout, glabrous or puberulous at the base; basal leaves petiolate, lanceolate, spatulate, or ovate, glabrous or puberulous, stem leaves 5 to 14 cm. long, narrowly linear to broadly lanceolate; calyx 6 to 10 mm. long, lobes broadly lanceolate, elliptic, or ovate, acute to short accuminate, margins scarious; corolla 28 to 38 mm. long, scarlet, strongly bilabiate, throat gradually and moderately inflated, upper lobes projecting, the sinus very short, lower lobes long and narrow, reflexed and bearded at the base with long, loose, yellow hairs or sometimes bearding scant; anthers exserted, dehiscent most of their length, minutely denticulate on the edges; staminode included, glabrous, only slightly dilated at the tip. Figure 49.

Specimens examined: ARIZONA. *Cochise County:* Chiricahua National Monument, June 12, 1946, *Reed 194* (UNM). *Pima County:* Wrightson Peak, Santa Rita Mountains, September 1, 1944, *Clark 12312* (UNM). NEW MEXICO. *Catron County:* 20 miles south of Luna, June 21, 1940, *Turner* and *Nisbet 789* (UNM); Gila Cliff Dwellings, July 5, 1952, *Dunn 8353* (UNM). *Grant County:* 10 to 15 miles north of Dwyer, June 24, 1940, *Turner* and *Nisbet 788* (UNM). *Hidalgo County:* South of Cloverdale, June 5, 1948, *Dittmer 5815* (UNM). *Sierra County:* Black Range, September 10, 1950, *Clark 3340* (UNM).

The range of *P. barbatus* ssp. *barbatus* extends from northern Mexico through southwestern New Mexico and Arizona into Utah. In Catron, Socorro, and Sierra counties of New Mexico, it shows evidence of hybridization with *P. barbatus* ssp. *torreyi* in that the sepals may be intermediate in length and the amount and coloring of the bearding in the throat may vary. Among plants collected at Emory Pass, Mimbres Mountains, western Sierra County, one plant (*Jackson* and *Nisbet 1176,* UNM) has sepals 6 to 8 mm. long and scant to heavy bearding in the throat of the corolla; another plant (*Jackson* and *Nisbet 1177,* UNM) has sepals only 5 mm. long and no bearding in the throat of the corolla. Plants from the Mogollon and Pinos Altos mountains of Catron and Grant counties vary from typical *P. barbatus* ssp. *barbatus* to typical *P. barbatus* ssp. *torreyi;* some specimens (*Castetter 5817, Dunn 8260,* UNM) could be assigned to either entity with equal propriety. This subspecies flowers from June to September in the pinon-juniper-oak woodlands and at higher elevations in the coniferous forests up to 10,000 feet. In the irrigated valleys it is sometimes seen along the fence rows and highways. The amount of puberulence varies and is not a constant characteristic over any section of the range.

12. *Penstemon barbatus* ssp. *Torreyi* (Benth.) Keck, Jour. Wash. Acad. Sci. 29:491. 1939.

Penstemon torreyi Benth., DC. Prod. 10:324. 1846.
Penstemon barbatus var. *torreyi* A. Gray, Proc. Amer. Acad. Arts and Sci. 6:59. 1862.

Very similar to *P. barbatus* ssp. *barbatus,* but usually the stems more slender, the foliage less ample, and the stem leaves linear; calyx 3 to 5 mm. long; corolla glabrous at the base of the lower lobes or with a few white or yellowish hairs. Figure 83.

Specimens examined: ARIZONA. *Coconino County:* Coulton Ranch, Flagstaff, July 21, 1935, *Whiting 756/1183* (UNM). COLORADO. *Los Animas County:* Monument Lake, July 9, 1952, *Williams* (UNM). NEW MEXICO. *Bernalillo County:* Cedro Canyon, July 3, 1940, *Nisbet 752* (UNM). *Catron County:* Gila Cliff Dwellings, July 5, 1952, *Dunn 8329* (UNM). *Colfax County:* Cimarron Canyon, August 2, 1940, *Nisbet 784* (UNM). *Dona Ana County:* Dripping Springs, Organ Mountains, September 30, 1935, *Hershey* and *Nisbet 694* (UNM). *Eddy County:* Guadalupe Mountains, August 16, 1939, *Hershey* and *Nisbet 693* (UNM). *Grant County:* Cherry Creek Springs, June 23, 1939, *Hershey* and *Nisbet 696* (UNM). *Lincoln County:* White Mountains, June 20, 1939, *Worth* and *Nisbet 717* (UNM). *Mora County:* Ocate, July 3, 1939, *Nisbet 666* (UNM). *Otero County:* Cloudcroft, July 4, 1938, *Hershey* and *Nisbet 695* (UNM). *Rio Arriba County:* Rio de los Pinos, July 5, 1942, *Castetter 5820* (UNM). *Sandoval County:* Jemez Mountains, August 9, 1930, *Castetter 5811* (UNM). *San Miguel County:* El Porvenir, August 24, 1910, *Wooten* (UNM). *Sierra County:* Hillsboro, July 31, 1941, *Hershey 3521* (UNM). *Socorro County:* Magdalena Mountains, July 6, 1940, *Nisbet 875* (UNM). *Taos County:* Holman Hill, July 3, 1939, *Nisbet 47* (UNM); Costilla Canyon, July 18, 1953, *Castetter 5806* (UNM). *Union County:* Sierra Grande, July 30, 1940, *Nisbet 775* (UNM).

Subspecies *torreyi* blooms from June to August and occasionally in September at higher elevations. Even when rainfall is unusually light, it flowers persistently. Its range is central Colorado and southward through New Mexico on both sides of the continental divide. This subspecies is not common on the western slope of the continental divide nor in Arizona. In the Sangre de Cristo, Jemez, Sandia, Manzano, and Magdalena mountains, *P. barbatus* ssp. *torreyi* is one of the more common summer flowers. It is uncommon in the White, Sacramento, and Guadalupe mountains. From Catron County northward, ssp. *torreyi* is largely replaced by ssp. *trichander.*

13. *Penstemon barbatus* ssp. *trichander* (A. Gray) Keck, Jour. Wash. Acad. Sci. 29:491. 1939.

Penstemon barbatus var. *trichander* A. Gray, Proc. Amer. Acad. Arts and Sci. 11:94. 1876.
Penstemon trichander Rydb., Bull. Torr. Bot. Club 33:151. 1906.

Distinguished from *P. barbatus* ssp. *barbatus* and *P. barbatus* ssp. *torreyi* by the long white hairs on the anthers, this pubescence sometimes sparse. Figure 48.

Specimens examined: ARIZONA. *Apache County:* Navajo Reservation, July 2, 1935, *Starr SCS A 481* (UNM). NEW MEXICO. *Catron County:* West of Datil, July 16, 1944, *Hershey 3199* (UNM). *McKinley County:* South of Crownpoint, August 6, 1941, *Hershey 3513* (UNM); Near Chuska Peak, summer, 1934, *SCS* (UNM). *Rio Arriba County:* 20 miles south of Tierra Amarilla, July 22, 1949, *Dittmer* and *Castetter 5818* (UNM). *San Juan County:* Washington Pass, Chuska Mountains, July 2, 1955, *Castetter 8638* (UNM). *Socorro County:* Santa Monica Canyon, July 5, 1940, *Nisbet 771* (UNM). *Valencia County:* Mount Taylor, July 25, 1952, *Castetter* and *Dittmer 5814* (UNM).

The range of ssp. *trichander* extends from southern Utah and southwestern Colorado to northeastern Arizona and northwestern New Mexico. Specimens from Sandoval, Valencia, Socorro, and Catron counties are usually lightly bearded on the anthers. Of a number of specimens collected within a few yards of each other at Santa Monica Ranger Station, San Mateo Mountains, Socorro County, some are typical ssp. *torreyi* (*Nisbet 769*, UMN) with sepals 3 to 4 mm. long, little or no bearding in the throat of the corolla, and no pubescence on the anthers; others have sepals 4 to 5 mm. long, little or no bearding in the throat of the corolla, and light pubescence on the anthers (*Nisbet, 771*, UNM).

14. *Penstemon buckleyi* Pennell, Proc. Acad. Nat. Sci. Phila. 73:486. 1921.

Penstemon amplexicaulis Buckley, Proc. Acad. Nat. Sci. Phila. 13:461. 1862.

Stems 3 to 4 dm. tall, solitary or few, stout, glabrous and glaucous, not or only slightly blackening in drying; leaves moderately thick, glabrous and somewhat glaucous, basal leaves mostly oblanceolate or spatulate, obtuse, but a few leaves lanceolate and acute, all with margined petioles, stem leaves sessile, lanceolate to ovate, acute; inflorescence narrow, not secund, peduncles and pedicels short, each peduncle with several flowers, bracts broadly ovate, the bases often truncate to subcordate, the apices acute, obtuse, or retuse, mucronate; calyx 4 to 5 mm. long, glabrous, base of each lobe ovate and the tip short to long acuminate, margins scarious; corolla 16 to 20 mm. long, pale lavender or pale blue, with dark guide lines, throat gradually and slightly expanded, lobes 3 to 4 mm. long, spreading; anther sacs narrow, completely dehiscent, not explanate; staminode moderately dilated, sparsely to moderately bearded with yellowish hairs. Figures 50, 51.

Specimens examined: NEW MEXICO. *Chavez County:* Near Lake Arthur, summer 1936, Grazing Survey Herbarium, File *329* (UNM). *Lea County:* Short distance north of Oil Center, May 30, 1955, *Castetter 7568* (UNM). TEXAS. *Wheeler County:* East of Shamrock, April 12, 1946, *Clark 13118* (UNM).

Penstemon buckleyi is very similar in appearance and closely related to *P. angustifolius* ssp. *caudatus* from which it can be distinguished by its paler flowers, sparsely bearded staminode, and bracts that lack the caudate tip. *Penstemon buckleyi* is a spring blooming species growing in sandy soil of the grasslands from western Kansas to western Texas and southeastern New Mexico.

15. *Penstemon angustifolius* ssp. *caudatus* (Heller) Keck, Jour. Wash. Acad. Sci. 29:490. 1939.

Penstemon caudatus Heller, Minn. Bot. Stud. 2:34. 1899. The type was collected May 26, 1897, at Barranca in southwestern Taos County by Heller.

Penstemon angustifolius var. *caudatus* Rhdb., Bull. Torr. Bot. Club 33:151, 1906.

Penstemon angustifolius ssp. *venosus* Keck, Jour. Wash. Acad. Sci. 29:490. 1939.

Plants glabrous throughout, glaucous, both stems and leaves sometimes blackening in drying; stems 2 to 5 dm. tall, stout, one to several; basal leaves lanceolate, spatulate, or oblanceolate, short petiolate, usually narrower than the stem leaves or the lowest bracts, middle and upper stem leaves 3.5 to 11 cm. long, 0.6 to 2.5 cm. wide, broadly lanceolate, acuminate; inflorescence usually compact, not secund, many-flowered, peduncles and pedicels short, lower bracts large, upper ones diminished in size, lanceolate to broadly ovate with an acuminate or caudate tip; calyx 4 to 7 mm. long, lobes lanceolate or narrowly ovate, acute to acuminate, margins broadly scarious on the lower half; corolla 17 to 23 mm. long, sky-blue, pale violet-blue, or almost pink, color variable in one inflorescence, throat gradually expanded, 6 to 8 mm. wide when pressed, lobes nearly equal and spreading, usually glabrous but occasionally the lower lip with a few short hairs at the base; anther sacs narrow, not explanate, completely dehiscent; staminode dilated, bearded with deep yellow hairs more numerous near the tip. Figure 52.

Specimens examined: NEW MEXICO. *Colfax County:* Springer, May 13, 1939, *Nisbet 30* (UNM); Johnson's Mesa, May 28, 1940, *Nisbet 739* (UNM). *McKinley County:* Crownpoint, May 21, 1940, *Gooding 10846* (UNM). *San Juan County:* 10 to 15 miles south of Bloomfield, June 18, 1953, *Castetter 8226;* June 29, 1957, *Nisbet 1131* (UNM); Cedar Hills, north of Aztec, June 9, 1953, *Castetter 8223* (UNM); Chaco Canyon National Monument, June 15, 1945, *Clark 12766* (UNM). *Taos County:* Barranca, *Heller 3851* (MIN); 7 miles south of Tres Piedras, July 8, 1955, *Nisbet 10454* (UNM). *Union County:* Capulin Mountain near top, June 20, 1951, *Castetter 8224* (UNM); Emory Gap, May 28, 1940, *Nisbet 737* (UNM); Breaks of Dry Cimmaron, May 16, 1952, *Castetter 5805* (UNM).

In southern Colorado *P. angustifolius* ssp. *caudatus* meets and intergrades with *P. angustifolius* ssp. *angustifolius.* In New Mexico ssp. *caudatus* is ordinarily distinct, but there is much variation in the height of the plants and the size of the stem leaves and lower bracts. Some few specimens approach the northern form as they have very long narrow leaves and bracts that are only slightly widened at the base. However, most New Mexican plants of ssp. *caudatus* have tall, thick stems, many flowers, and upper stem leaves and bracts that are broad and caudate.

Subspecies *venosus* was proposed by Keck on the basis of "smaller, often pinkish flowers, and the more venose bracts, which do not turn blackish in drying." The smaller and pinkish flowers seem to occur more frequently in the western forms but do occur among the eastern populations. The prominently veined bracts and leaves appear sporadically in the western forms and occasionally in the eastern forms. One sheet of *P. angustifolius* ssp. *caudatus* (*Nisbet 30,* UNM) from Springer, Colfax County, contains two stalks from the same root system; one stalk shows blackening of the leaves and bracts, the other does not. Several sheets of the western form show considerable blackening of leaves and bracts (*Castetter 8226, Nisbet 1131,* UNM).

Penstemon angustifolius ssp. *caudatus* grows in sandy soil in northern Arizona, southern Utah, southern Colorado, northern New Mexico, and western Kansas. It is a common spring blooming species on the plains and foothills of the northern tier of counties in New Mexico.

16. *Penstemon secundiflorus* Benth., DC. Prod. 10:325. 1846.

Stems 1.5 to 5 dm. tall, one to several; the whole plant glabrous and somewhat glaucous; leaves firm, often mucronate, those of the stem lanceolate to lance-ovate, acute, erect, occasionally spreading, those of the basal rosette obovate to spatulate, petiolate, obtuse; inflorescence narrow, secund, bracts lanceolate, erect, the lower leaflike and the upper diminished in size; calyx 4 to 7 mm. long, lobes lanceolate to ovate, acute, the scarious margins often pinkish or purplish; corolla 17 to 25 mm. long, dark blue or strongly shaded with violet, often appearing red-violet in the field, throat gradually expanded to 10 mm. wide, lower lip more or less bearded; anther sacs narrow, not explanate; staminode dilated, heavily bearded on the upper side with yellow hairs. Figures 53, 55, 84.

Specimens examined: COLORADO. *El Paso County:* Near Monument, route 85, June 5, 1956, *Nisbet 11114* (UNM). *Pueblo County:* 20 miles north of Walsenburg, route 85, June 5, 1956, *Nisbet 11112* (UNM). NEW MEXICO. *Bernalillo County:* Cedro Canyon, Sandia Mountains, May 28, 1932, *Castetter 5869* (UNM); Escabosa, June 2, 1940, *Nisbet 726* (UNM). *Colfax County:* Route 21, south of Cimarron, May 14, 1939, *Nisbet 26* (UNM). *Harding County:* 8 to 10 miles north of Mills, May 22, 1939, *Nisbet 27* (UNM). *Sandoval County:* Lower Jemez Canyon, May 30, 1931, *Castetter 5872* (UNM). *San Miguel County:* 8 to 12 miles north of Las Vegas, May 29, 1941, *Nisbet 826* (UNM). *Santa Fe County:* Apache Canyon, east of Santa Fe, May 18, 1952, *Castetter 5868* (UNM). *Taos County:* Roadcut, Taos side of U. S. Hill, July 2, 1955, *Nisbet 9414* (UNM). *Union County:* Emory Gap, May 28, 1940, *Nisbet 720* (UNM).

Penstemon secundiflorus occurs on the eastern continental slope from Bernalillo County, New Mexico, northward through Colorado, and into southern Wyoming, on gravelly or rocky ridges of the grasslands, on bushy slopes of the lower mountains, or in the open parks. There is considerable indication that in those areas where *P. secundiflorus* and *P. fendleri* grow in close proximity that there has been some exchange of genes.

17. *Penstemon fendleri* Torr. and Gray, U. S. Rpt. Expl. Miss. Pacif. 2:168. 1855. The type was collected on the Pecos and Llano Estacado in 1854.

Stems 2 to 5 dm. tall, solitary or few, the whole plant glabrous and somewhat glacous; leaves thick and firm, usually mucronate, basal leaves lanceolate, elliptic, or narrowly ovate, short petiolate, mostly obtuse, stem leaves usually spreading, lanceolate to ovate, upper ones shorter and broader than lower; inflorescence narrow, not secund, the short and erect peduncles and pedicels usually much shorter than the internodes, thus producing an open inflorescence (will not hold for short plants), bracts narrowly to broadly ovate, acute or with an abruptly pointed tip, lower ones leaflike, upper ones much reduced in size; calyx 4 to 7 mm. long, lobes ovate, acute to acuminate, broadly scarious margined; corolla 17 to 25 mm. long or occasionally longer, usually violet but sometimes blue, throat glabrous with prominent dark violet guide lines, narrow and usually somewhat curved, expanded slightly at and near the orifice, lobes spreading; anther sacs narrow, completely dehiscent, not explanate; staminode dilated, heavily bearded with yellow hairs at and near the tip. Figures 54, 56.

Specimens examined: MEXICO: CHIHUAHUA. Benton's Ranch, May 7, 1940, *Hershey 3505* (UNM). OKLAHOMA. *Jackson County:* Breaks of Red River, near Eldorado, April 4, 1953, *Waterfall 11259* (UNM). NEW MEXICO. *Chavez County:* 5 to 6 miles north Roswell, April 27, 1956, *Nisbet 11109* (UNM). *DeBaca County:* 5 miles north of Fort Sumner, May 30, 1941, *Nisbet 830* (UNM). *Dona Ana County:* Organ Mountains, April 7, 1935, *Hershey* and *Nisbet 687* (UNM). *Grant County:* Silver City, May 10, 1939, *Nisbet 35* (UNM). *Guadalupe County:* Pastura, June 6, 1941, *Nisbet 846* (UNM). *Harding County:* David Hill, May 22, 1939, *Nisbet 33* (UNM). *Hidalgo County:* Animas Mountains, San Luis Pass, May 14, 1955, *Castetter 7566* (UNM). *Lincoln County:* Corona, June 9, 1941, *Nisbet 839* (UNM). *Lea County:* Near Lovington, April 27, 1956, *Nisbet 11106* (UNM). *Luna County:* By Florida Mountains, April 10, 1937, *Hershey 10850* (UNM). *Mora County:* 15 miles southwest of Wagon Mound, May 29, 1941, *Nisbet 825* (UNM). *Quay County:* Logan, May 22, 1939, *Nisbet 34* (UNM). *Sandoval County:* Water Canyon, Jemez Mountains, May 25, 1931, *Castetter 5826* (UNM). *San Miguel County:* 12 miles south of Las Vegas, June 18, 1955, *Nisbet 1153* (UNM). *Sierra County:* Hillsboro, May 6, 1904, *Metcalf 1157* (UNM). *Socorro County:* San Antonio, south of Socorro, April 22, 1933, *Nelson 5828* (UNM).

Penstemon fendleri is a spring blooming species, flowering as early as April in the southern part of the state but not until May and June in the northern part. It is found in sandy or gravelly soil in grasslands of the plains or lower mountains. The range extends from western Oklahoma and Texas across New Mexico to southeastern Arizona and northern Chihuahua. The type locality, "on the Staked Plains," may have been in eastern New Mexico or in western Texas.

18. *Penstemon ambiguus* Torr. ssp. *ambiguus,* Ann. Lyc. Nat. His. N. Y. 2:228. 1828.
Leiostemon ambiguus Greene, Leaflets 1:223. 1906.

Stems 2 to 6 dm. tall, profusely branched, woody well above the base, puberulous; leaves 6 to 30 mm. long, linear, mucronate, usually inrolled, puberulous or glabrous, scabrescent on the edges; inflorescence of each branch narrow, peduncles one- or two-flowered, bracts resembling the leaves or more subulate; calyx 2 to 3 mm. long, lobes ovate, acute, scarious margined; corolla 15 to 24 mm. long, pale to deep pink, or almost orchid externally, the face of the lobes glistening white, the curved throat narrow, 3 mm. wide at the orifice, the convex upper surface from 2.5 to 4 mm. shorter than the lower surface, lobes rounded, upper ones reflexed and lower projecting, thus the face of the lobes lying close to a horizontal position, orifice bearded with short hairs at the base of all lobes, the hairs running in two lines down the lower side of the thorat, prominent guide lines present; stamens included, anther sacs small, explanate; staminode included, glabrous, not dilated. Figures 57-59.

Specimens examined: TEXAS. Near Amarillo, June 15, 1937, *Nisbet 713* (UNM). NEW MEXICO. *Bernalillo County:* Albuquerque Arroyo, June 20, 1930, *Castetter 5798* (UNM). *Curry County:* 18 miles northwest of Melrose, July 14, 1951, *Dittmer 5800* (UNM). *DeBaca County:* 5 miles north of Fort Sumner, May 31, 1955, *Nisbet 1138* (UNM). *Guadalupe County:* 6 to 8 miles south of Santa Rosa, June 6, 1941, *Nisbet 844* (UNM). *Lea County:* Texas line south of Jal, May 3, 1955, *Castetter 7565* (UNM). *Quay County:* One mile west of Tucumcari, June 7, 1951, *Hoff 5802* (UNM). *Roosevelt County:* Pep, July 30, 1938, *Hershey* and *Nisbet 699* (UNM). *Santa Fe County:* Mesa between Bernalillo and Santa Fe, June 10, 1939, *Nisbet 664* (UNM). *Torrance County:* 8 miles southeast of Gran Quivera, July 3, 1940, *Nisbet 750* (UNM). *Union County:* 25 miles southwest Clayton, June 14, 1939, *Nisbet 663* (UNM).

Commonly called the bush penstemon, *P. ambiguus* is found in the sand hills and on sandy plains and mesas of eastern Colorado, western Oklahoma, western Texas, and eastern and central New Mexico as far west as Albuquerque. From Socorro southward in the Rio Grande Valley and in southwestern New Mexico, ssp. *ambiguus* is replaced by ssp. *laevissimus. Penstemon ambiguus* blooms from May to August. Under cultivation at Springer, Colfax County, the plants were a mass of pink and white blooms in June and much of July with some flowers persisting through August and until frost in September.

19. *Penstemon ambiguus* × *thurberi* Nisbet and Jackson, hybr. nov.
Plantis propriis mediis diverse inter Penstemon ambiguus et P. thurberi.

Stems moderately puberulous or glabrate; leaves inrolled, glabrous except for the minutely scabrescent edges; corolla 12 to 15 mm. long, 3.5 to 5 mm. wide, not curved and gradually expanded, or somewhat curved and remaining narrower, color of the lobes varying from glistening white to blue-purple, the throat and tube pale pink to deep reddish purple, pubescence of the throat as in *P. ambiguus* or sparse in the upper throat as in *P. thurberi.*

Type: NEW MEXICO. *Socorro County:* 17 to 20 miles west of Socorro, route 60, June 15, 1956, *Jackson* and *Nisbet 1158* (UNM).

Specimens examined: NEW MEXICO. *Lincoln County:* 3 miles north of Carrizozo, June 9, 1941, *Nisbet 834* (UNM). *Socorro County:* 17 miles west of Socorro, June 9, 1939, *Nisbet 42 43 44* (UNM); 17 to 20 miles west of Socorro, route 60, June 15, 1956, *Jackson* and *Nisbet 1159, 1160* (UNM).

West of Socorro, Socorro County, hybrids of this combination form an extensive colony along the highway drainage. The colony of hybrids north of Carrizozo, Lincoln County, found in 1941, has apparently fallen prey to drought and overgrazing. However, plants in that vicinity may make a comeback whenever moisture conditions are better. A discussion of this hybrid combination is contained in the section on hybridization.

20. *Penstemon ambiguus* ssp. *laevissimus* Keck, Jour. Wash. Acad. Sci. 29:491. 1939.

This subspecies differs from typical *P. ambiguus* in having glabrous stems and the edges of the glabrous leaves smooth or remotely and very minutely scabrescent.

Specimens examined: ARIZONA. *Coconino County:* Leupp, north of Winslow, July 19, 1934, *Oakey, SCS A65* (UNM). TEXAS. *El Paso County:* East of El Paso, August 8, 1931, *Clark 4300* (UNM). NEW MEXICO. *Eddy County:* 20 miles east of Carlsbad, June 5, 1952, *Castetter* and *Dittmer 5803* (UNM). *Luna County:* Deming, June 22, 1939, *Hershey* and *Nisbet 698* (UNM). *Socorro County:* Short distance north of Abeyas, July 7, 1940, *Nisbet 756* (UNM); Sandy bottoms south of Socorro, June 12, 1950, *Clark 15401* (UNM).

The range of ssp. *laevissimus* extends from Socorro County south through the Rio Grande Valley, east to Texas, and west to Arizona and Nevada.

21. *Penstemon thurberi* Torr., U. S. Rpt. Expl. Miss. Pacif. 7:15. 1856.

Leiostemon thurberi Greene, Leaflets 1:223. 1906.

Stems 2 to 4 dm. tall, branched, woody well above the base, glabrate; leaves 5 to 25 mm. long, almost filiform, mucronate, glabrous, edges minutely scabrescent; inflorescence of each branch narrow, each peduncle usually one-flowered, bracts resembling the leaves, becoming shorter at the upper nodes; calyx 2 mm. long, lobes ovate, acute, scarious margined; corolla 10 to 14 mm. long, blue- or red-purple, throat not curved, gradually expanded to 4 or 5 mm. wide (these measurements of fresh flowers), lobes spreading, lightly pubescent at the base of the lower lobes and in two lines down the lower throat, sometimes also pubescent around the upper sinuses; anther sacs very small, explanate; staminode very narrow, glabrous. Figures 60, 61.

Specimens examined: NEW MEXICO. *Catron County:* Near Datil, July 16, 1944, *Hershey 3172* (UNM). *Hidalgo County:* Granite Gap, Little Hatchet Mountains, August 24, 1955, *Castetter 9979* (UNM); East of Lordsburg, May 30, 1932, *Clark 4795* (UNM). *Luna County:* Gage, June 23, 1956, *Jackson* and *Nisbet 1155* (UNM).

Penstemon thurberi flowers from April to August in scattered colonies in the desert grasslands. The time of flowering depends largely upon the available moisture. This species seems to be uncommon, but its range includes southern California, southern Arizona, southwestern New Mexico, and northern Mexico.

22. *Penstemon linarioides* A. Gray ssp. *linarioides,* U. S. and Mex. Bound. Bot. Rpt. 112, 1859. The type was collected near the copper mines at Santa Rita, Grant County, by Wright.

Stems 2 to 5 dm. tall, few to several, erect or ascending from a woody base, stems and leaves puberulous with fine, appressed or scalelike hairs, sometimes glabrate; leaves linear, mucronate, 10 to 25 mm. long, 1.5 to 2 mm. wide, crowded on the base of the flowering stems and on sort sterile shoots, scattered on flowering stems above the base; inflorescence glandular-pubescent, narrow, secund, bracts small, subulate, the one or occasionally two peduncles at each node bearing one to several flowers; calyx 4 to 7 mm. long, lobes ovate, scarious margined below the acute to short acuminate tip (tip .5 to 2 mm. long); corolla 16 to 20 mm. long, bright blue with purplish or violet tube and throat or the complete flower pale to dark violet with deep purple guide lines, tube slender, the two-ridged throat abruptly and moderately to widely expanded on the upper side, strongly bearded with yellowish hairs at the base of the lower lobes; anther sacs oblong, opposite, completely dehiscent, not explanate; staminode narrow, bearded for most of its length with bright yellow hairs which are longer and tufted at the tip. Figures 62, 63, 84.

Specimens examined: ARIZONA. *Cochise County:* Chiricahua National Monument, July 16, 1946, *Reed 233* (UNM). *Greenlee County:* 15 miles north of Clifton, June 22, 1958, *Nisbet 1180* (UNM). NEW MEXICO. *Catron County:* Largo Canyon, near Reserve, August 7, 1952, *Castetter 5842* (UNM). *Dona Ana County:* Organ Mountains, *Hershey* (NMC). *Grant County:* 2 miles north of Silver City, June 22, 1940, *Turner* and *Nisbet 786* (UNM); White Signal, August 11, 1946, *Clark 14030* (UNM). *Hidalgo County:* Maverick Canyon, east slope of Peloncillo Mountains, August 22, 1955, *Castetter 9920* (UNM). *Luna County:* East of Hachita, June 14, 1948, *Castetter 5841* (UNM). *Sierra County:* South Percha Canyon, Mimbres Mountains (Forest Service herbarium, Albuquerque). *Socorro County:* Water Canyon, Magdalena Mountains, July 20, 1958, *Nisbet 2014* (UNM).

Several more or less distinct forms of *P. linarioides* occur in Arizona, but only ssp. *linarioides,* ssp. *coloradoensis,* and possibly ssp. *maguirei* occur in New Mexico. Table 3 summarizes and contrasts the chief taxonomic characteristics of the members of the section *Ericopsis* which are found in New Mexico. Because its presence in New Mexico is doubtful, ssp. *maguirei* is not included in the table.

Penstemon linarioides ssp. *linarioides* blooms from June to August in open grassy spaces or on rocky hillsides among pinons, junipers, and oaks and among the pines at higher elevations. Its range is southwestern New Mexico and southeastern Arizona.

23. *Penstemon linarioides* ssp. *maguirei* Keck, Bull. Torr. Bot. Club 64:378. 1937.

Similar to *P. linarioides* ssp. *linarioides* except leaves oblanceolate, lower ones 2.5 to 5 mm. wide, obtuse, acuminate to the base.

The type locality is “on limestone cliff sides 1 mile west of Metcalf, Greenlee County, Arizona.” Metcalf is an abandoned mining camp and the cliffs one mile west are now entirely covered by the tailings of the Morenci Copper Mines.

No specimens of this subspecies have been examined and it is very doubtfully included with New Mexican penstemons. Keck (1937a) cites the following specimen: "Grant County, Gila Valley, Nov. 1880, *Greene* (Po)." In the summer of 1938 an unsuccessful effort was made to find this subspecies in the Gila Valley.

24. *Penstemon linarioides* ssp. *coloradoensis* (A. Nels.) Keck, Bull. Torr. Bot. Club 64:375. 1937.

Penstemon coloradoensis A. Nels., Bull. Torr. Bot. Club 26:355. 1899.

Flowering stems 1 to 3.5 dm. tall, numerous, erect or ascending from a branching rootstock or from older stems that have become decumbent and rooted underneath, thus forming small mats; corolla 15 to 20 mm. long, lightly bearded at the base of the lower lobes; staminode bearded at the tip with a tuft of bright yellow hairs and behind the tuft with sparse white or yellowish hairs. Figure 65.

Specimens examined: COLORADO. *Montezuma County:* 2 to 3 miles north of Mancos, June 29, 1957, *Jackson* and *Nisbet 1136* (UNM); 2 miles west of Mancos, June 29, 1957, *Jackson* and *Nisbet 1137* (UNM). NEW MEXICO. *McKinley County:* McGaffey, July 4, 1955, *Castetter 8681* (UNM); Mexican Springs, June 25, 1934, (Herbarium of SCS, UNM). *San Juan County:* Near state line, north of Cedar Hill, June 9, 1953, *Castetter 5845* (UNM); Washington Pass, Chuska Mountains, July 2, 1955, *Castetter 8652* (UNM).

Subspecies *coloradoensis* has been regarded as a species by Pennell (1920) and by Rydberg (1917), but it was considered a subspecies by Keck (1937a). In habit ssp. *coloradoensis* resembles *P. crandallii* ssp. *glabrescens;* but in the type of puberulence and characteristics of the inflorescence, it is definitely related to *P. linarioides.* The distinguishing characteristics of this subspecies do not hold for all plants. The amount and type of puberulence may vary considerably. Some plants are so heavily puberulous with scalelike hairs that the leaves appear grayish; others are glabrate or the pubescence may be of intermingled flat, scalelike hairs and fine, erect or retrorse hairs. Some plants from westcentral New Mexico have longer bracts in the inflorescence and longer tips on the calyx lobes than are typical of ssp. *coloradoensis.*

Specimens of ssp. *coloradoensis* (*Jackson* and *Nisbet 1136, 1137,* UNM) which were collected at the type locality near Mancos, Colorado, and examined carefully in the field are all two-ridged in the throat as are those from the Chuska Mountains (*Castetter 8652,* UNM) and from McGaffey (*Castetter 8681,* UNM). Plants from these two latter localities were also examined while fresh and Chuska Mountain plants were grown in gardens for two years.

Flowers from plants of *P. linarioides* var. *viridis* (*Nisbet 1159,* UNM) from near Springerville, Arizona, are two-ridged in the throat. The same thing is true for specimens of this variety collected 5 miles west of Miami, Gila County, Arizona (*Nisbet 1144,* UNM). Flowers from plants of *P. linarioides* ssp. *linarioides* (*Clark 14030,* UNM) from near White Signal, Grant County, New Mexico, retained the folds in the lower throat when boiled. Corollas of *P. linarioides* ssp. *linarioides* were examined in the field at the following localities and all were found to be two-ridged on the lower throat: Arizona: Apache Pass, Cochise County; 15 miles north of Clifton, Greenlee County (*Nisbet 1180,* UNM). New Mexico: 12 miles south of Reserve, Catron County (*Nisbet 2013, 2016,* UNM); Water Canyon, Magdalena Mountains, Socorro County (*Nisbet 2014,* UNM). This same characteristic was observed in *P. linarioides* ssp. *sileri* (*Nisbet 1186,* UNM) collected near Prescott, Arizona. Keys and descriptions that have described the subspecies of *P. linarioides* as "throat rounded and not two-ridged in the throat" are evidently in error.

25. *Penstemon crandallii* ssp. *glabrescens* (Pennell) Keck, Bull. Bot. Club 64:369. 1937.
Penstemon glabrescens Pennell, Contr. U. S. Nat. Herb. 20:375. 1920.

Stems several to many, 9 to 25 cm. tall, ascending, puberulous with fine erect hairs or more often the hairs retrorse, woody older stems becoming decumbent and often rooting at the lower nodes; leaves linear, mucronate, 10 to 35 mm. long, 1 to 3 mm. wide, those on sterile shoots crowded and smaller, puberulous at the base and in a median line on the dorsal side, otherwise glabrous; inflorescence secund, glandular-pubescent, one peduncle at a node bearing one to three flowers, bracts leaflike and not reduced in size except at two or three upper nodes; calyx 5 to 8 mm. long, the base of the lobes ovate, scarious and more or less erose, the tip long acuminate to caudate, often as long as the base; corolla 17 to 23 mm. long, bilabiate, the throat little longer than the tube, upper throat rounded, the lower flattened and two-ridged, lightly pubescent at the orifice, guide lines usually present, lobes usually blue, throat and tube blue- or red-purple; anthers narrow, completely dehiscent, not explanate, minutely denticulate on the edges; staminode slender, pubescent most of its length with bright golden hairs, longer and tufted at the tip. Figures 66-68, 85.

Specimens examined: NEW MEXICO. *Colfax County:* Merino Valley, August 9, 1941, *Nisbet 862* (UNM). *Sandoval County:* 3 miles northwest of Cuba, June 29, 1957, *Jackson* and *Nisbet 1130*

(UNM). *Rio Arriba County:* El Vado Lake, June 20, 1941, *Mankin* and *Nisbet 850* (UNM); Mountains east of Regina, June 21, 1941, *Mankin* and *Nisbet 854* (UNM). *Taos County:* 7 miles south of Tres Piedras, July 8, 1955, *Nisbet 10469* (UNM); Road cut 5 miles south of Questa, July 1, 1955, *Nisbet 8662* (UNM); Penasco Valley July 2, 1955, *Nisbet 8663* (UNM); Taos Canyon, August 3, 1941, *Nisbet 859* (UNM).

Penstemon crandallii ssp. *glabrescens* differs from ssp. *crandallii* by its longer stems, narrower and often more crowded leaves, and the wider scarious margins and caudate tips of the calyx lobes. Plants with the lower leaves not linear but oblong-spatulate and to 3 mm. wide have been found growing on roadcuts or under cultivation where maximum moisture is available and competition is at a minimum. In New Mexico the corrollas average as large as the measurements given for *P. crandallii* ssp. *crandallii* as it occurs in Colorado.

This subspecies blooms in June, July, and August in open areas in the pinon-juniper or pine woodlands, on banks of arroyos, on roadcuts, and sometimes at higher altitudes associated with spruce and fir. Subspecies *glabrescens* occurs in southcentral Colorado and northcentral New Mexico.

26. *Penstemon crandallii* ssp. *glabrescens* var. *taosensis* (Keck) Nisbet and Jackson, comb. nov.

Penstemon linarioides ssp. *taosensis* Keck, Bull. Torr. Bot. Club 64:373. 1937. The type was collected between Questa and Taos, Taos County, July 30, 1932, by Nelson.

Identical to *P. crandallii* ssp. *glabrescens* except the leaves are puberulous on both sides with fine erect or retrorse hairs.

Specimens examined: NEW MEXICO. *Rio Arriba County:* 2 miles west of Tres Piedras, July 8, 1955, *Nisbet 10476* (UNM); 15 miles southwest of Tres Piedras, July 8, 1955, *Nisbet 10470* (UNM); Truchas, July 5, 1942, *Camp 878* (UNM). *Taos County:* Penasco Valley, July 12, 1955, *Nisbet 8663* (UNM); 5 miles south of Questa, July 1, 1955, *Nisbet 8662* (UNM); U. S. Hill, June 30, 1939, *Nisbet 39* (UNM); San Cristobal, June 30, 1939, *Nisbet 38* (UNM).

Variety *taosensis* is apparently confined to Taos County, New Mexico, and closely adjacent parts of Rio Arriba County that lie to the south and west. It has not been found in pure stands but with populations of *Penstemon crandallii* ssp. *glabrescens.* Mass collections of these two forms have been made and studied in the field.

TABLE 3.—Tabulation of the characters of the New Mexican entities of *Penstemon crandallii* and *P. linarioides*.

	Penstemon crandallii		*Penstemon linarioides*	
	ssp. *glabrescens*	var. *taosensis*	ssp. *coloradoensis*	ssp. *linarioides*
Stems				
height	7 to 25 cm.	7 to 25 cm.	10 to 30 cm.	18 to 50 cm.
pubescence	fine, erect or retrorse	fine, erect or retrorse	scalelike, mostly appressed	scalelike, mostly appressed
growth habits	ascending, old stems decumbent and rooting at lower nodes	ascending, old stems decumbent and rooting at lower nodes	erect or ascending, old stems decumbent and rooting at lower nodes	mostly erect, sometimes ascending, rarely rooting at lower nodes
Leaves				
pubescence	glabrous on ventral side except at base	puberulous with erect or retrorse hairs	scalelike, mostly appressed hairs or rarely glabrate	scalelike, mostly appressed hairs
Inflorescence				
bracts	leaflike, not reduced in size except at 2 or 3 upper nodes	leaflike, not reduced in size except at 2 or 3 upper nodes	all reduced in size or leaflike at lowest node	all reduced in size or leaflike at lowest node
Calyx lobes				
shape	ovate, long acuminate or caudate	ovate, long acuminate or caudate	ovate or elliptical, acute to short acuminate	ovate or elliptical, acute or short acuminate
length	5 to 8 mm.	6 to 9 mm.	5 to 7 mm.	4 to 7 mm.
length of base	3 to 5 mm.	3.5 to 5 mm.	4 to 5.5 mm.	3 to 6 mm.
length of tip	2.5 to 4 mm.	2.5 to 5 mm.	.5 to 2 mm.	.5 to 2 mm.

TABLE 3.—Tabulation of the characters of the New Mexican entities of *Penstemon crandallii* and *P. linarioides*.—*Concluded*

	Penstemon crandallii		*Penstemon linarioides*	
	ssp. *glabrescens*	var. *taosensis*	ssp. *coloradoensis*	ssp. *linarioides*
Corolla				
shape	lower throat flattened and two-ridged, upper more or less inflated	lower throat flattened and two-ridged, upper more or less inflated	lower throat flattened and two-ridged, upper abruptly ampliate	lower throat flattened and two-ridged, upper abruptly ampliate
length	17 to 23 mm.	15 to 21 mm.	15 to 20 mm.	16 to 23 mm.
width	5 to 9 mm.	5 to 8 mm.	5 to 9 mm.	6 to 10 mm.
pubescence	few yellowish hairs at base of lower lobes	few yellowish hairs at base of lower lobes	few to many yellowish hairs at base of lower lobes	yellowish to golden hairs, moderately heavy at base of lower lobes
Staminode	golden hairs for most of length, longer at the tip	golden hairs for most of length, longer at the tip	golden hairs tufted at the tip, sparse yellowish hairs behind the tip	golden hairs most of length, longer and tufted at the tip

Keck distinguished var. *taosensis* from *P. crandallii* ssp. *glabrescens* "by its more ampliate corolla and by its taproot." Evidently the plants examined by Keck were in their first blooming season. Both forms have taproots when young, but old stems become decumbent and rooted at the lower nodes. However, neither entity forms mats of any size because of a tendency of the older parts of the plant to die out. As Table 3 shows, the corolla of var. *taosensis* is not more ampliate than that of ssp. *glabrescens.* Both are flattened and two-ridged on the lower throat while the dilation of the upper throat varies from a slight to a moderate amount. In fact, the two forms differ morphologically only in the pubescence of the leaves. The leaves of ssp. *glabrescens* are puberulous at the base and more or less on the dorsal side, but the leaves of var. *taosensis* are puberulous on both sides.

The designation of the form under discussion as a variety is cumbersome; however, the fact that its closest relationship is with *P. crandallii* ssp. *glabrescens* and not with *P. linarioides* is indubitable. In a recent experiment seeds of var. *taosensis* were planted under controlled conditions. Of eleven plants grown, seven have leaves that are puberulous as in var. *taosensis* and four have leaves that are glabrous ventrally and at the tip as in ssp. *glabrescens.* The information gained from this experiment combined with observations during a number of years of colonies containing both forms seems convincing proof that var. *taosensis* is a phenotype which generally occurs with a low frequency. However, one colony growing about 3 miles east of Truchas, Rio Arriba County, (*Nisbet 1194*, UNM) contained many more plants of var. *taosensis* than of ssp. *glabrescens.* In Colfax County colonies of ssp. *glabrescens* contain no plants of var. *taosensis.*

Penstemon linarioides ssp. *linarioides* Keck and *P. linarioides* ssp. *coloradoensis* (A. Nels.) Keck are included in Table 3 to show the large number of characteristics by which *P. crandallii* ssp. *glabrescens* var. *taosensis* differs from *P. linarioides* and also to suggest a probable relationship between *P. linarioides* and *P. crandallii* through *P. linarioides* ssp. *coloradoensis.* The more significant morphological similarities and differences are given in Table 3.

27. *Penstemon whippleanus* A. Gray, Proc. Amer. Acad. Arts and Sci. 6:73. 1862. The type was collected in an arroyo in the Sandia Mountains east of the Rio Grande by Bigelow in 1853.

Penstemon glaucous stenosepalus A. Gray, Proc. Amer. Acad. Arts and Sci. 6:70. 1862.

Penstemon arizonicus Heller, Bull. Torr. Bot. Club 26:591. 1899.

Penstemon stenosepalus (A. Gray) Howell, Fl. Northw. Amer. 1:514. 1901.
Penstemon metcalfei Woot. and Standl., Torreya 9:145. 1909.

Stems 1.5 to 6 dm. tall, few to several, slender, ascending or erect from horizontal woody rootstocks, puberulous or glabrous; leaves entire or denticulate, thin, glabrous, basal leaves ovate, spatulate, or lance-ovate, often long petiolate, stem leaves lanceolate or lance-oblong, acute, sessile; inflorescence glandular-pubescent, composed of 2 to 5 fascicles which are usually separated (at least the lower) by long internodes, lowest peduncles sometimes elongated, lower bracts leaflike, upper ones reduced in size; calyx 7 to 10 mm. long, lobes lanceolate, acute to long acuminate, glandular-pubescent, narrowly scarious margined near the base; corolla 22 to 30 mm. long, dull red-purple or dull blue-purple, the exterior glandular-pubescent, throat abruptly expanded, slightly contracted at the orifice, the villous lower lobes projecting and 3 to 5 mm. longer than the short upper lobes; anther sacs explanate; staminode not or very slightly dilated, glabrous or with a few yellowish hairs on and near the tip. Figure 69.

Specimens examined: ARIZONA. *Coconino County:* San Francisco Peaks, July 29, 1944, *Clark 12075* (UNM). COLORADO. *Archuleta County* (possibly Conejos County): San Juan Mountains, August 19, 1931, *Clark 4586* (UNM). NEW MEXICO. *Bernalillo County:* Cienage Canyon, Sandia Mountains, June 18, 1939, *Nisbet 873* (UNM); Sandia Crest, July 8, 1931, *Castetter 6077* (UNM). *Catron County:* Mogollon Mountains, August 9, 1952, *Castetter 6072* (UNM). *Lincoln County:* White Mountain Peak, Summer, 1939, *Worth* and *Nisbet 716* (UNM); Cold Springs, July 5, 1939, *Hershey* and *Nisbet 682* (UNM). *Mora County:* Upper Santa Barbara Canyon, July 2, 1939, *Nisbet 25* (UNM). *Rio Arriba County:* Cumbres Pass, July 23, 1949, *Castetter* and *Dittmer 6080* (UNM). *Sandoval County:* Redondo Mountains, August 9, 1931, *Castetter 6075* (UNM). *Santa Fe County:* Lake Peak Trail, July 29, 1953, *Castetter 2355* (UNM). *Sierra County:* Lookout Mine, south end of Black Range, May 2, 1905, *Metcalf 1605* (UNM). *Taos County:* Goose Lake below Gold Hill, August 13, 1955, *Castetter* and *Dittmer 9872* (UNM); On trail to Wheeler Peak, August 7, 1949, *Gordon* and *Norris 351* (UNM). *Torrance County: Manzano Mountains,* July 22, 1931, *Castetter 6074* (UNM). *Valencia County:* North slope of La Mosca Peak, July 27, 1952, *Castetter* and *Dittmer 6082* (UNM).

This species has been variously named in different localities, probably due to the variation in the pubescence of the stems, the amount of bearding on the staminode, and the color of the corolla. Reported colors for the corolla include dull white, lemon yellow, greenish brown, lavender, dull dark blue, bluish purple, and reddish purple. Only the bluish or reddish purple color has been found in New Mexico.

Penstemon whippleanus blooms from June to August or occasionally in September on wooded or grassy slopes in the yellow pine forests and upward to the alpine zone. It is found in Wyoming, Idaho, Colorado, Utah, Arizona, and New Mexico.

28. *Penstemon pulchellus* Lidl., Edwards Bot. Reg. 14: pl. 1138. 1828.

Stems medium in height, pubescent, somewhat woody at the base; leaves glabrous and of two kinds, the larger ones lanceolate or oblong, acute, definitely serrate, the smaller obscurely toothed leaves in fascicles in the axil of each larger leaf; inflorescence loose, glandular; corolla 20 to 25 mm. long, slightly glandular-pubescent externally, throat inflated, lightly pubescent at the base of the lower lobes; anther sacs explanate; staminode dilated and bearded at the tip with a tuft of short yellow hairs.

No specimens of *P. pulchellus* have been examined and no plants of this species have been collected in New Mexico for many years. Wooten and Standley (1915) state that it was collected in the San Luis Mountains by Mearns, probably in 1890 when Mearns was a naturalist with the second United States-Mexican Boundary Survey. Wooton and Standley gave the location of the San Luis Mountains as southern Grant County, but at that time southern Grant County extended to the Mexican boundary. The validity of this species seems to be questionable and certainly its existence in New Mexico is very doubtful. Considerable field work has been done in Southern Hidalgo County in the last few years, but this species has not been recollected. However, it has been thought best to continue to list *P. pulchellus* until its presence or absence in New Mexico can be definitely determined.

Penstemon companulatus (Cav.) Willd. is a closely related species of the highlands of central Mexico. Specimens of this species have been examined. The corollas of *P. campanulatus* are maroon-red while the corollas of *P. pulchellus* are thought to be violet with the underpart of the throat very pale.

29. *Penstemon jamesii* Benth, ssp. *jamesii*, DC. Prod. 10:325. 1846.
Penstemon similis A. Nels., Bull. Torr. Bot. Club 25:548. 1898.

Stems 1 to 5 dm. tall, one to several, glabrate or puberulous; leaves glabrate to strongly puberulous, entire, undulate, or irregularly serrate with a few short to elongated teeth, lower leaves petiolate, linear and acute, spatulate and obtuse, or lanceolate and tapering to both ends, stem leaves linear or lanceolate, acute; inflorescence narrow, secund, glandular-pubescent, bracts leaflike, upper ones gradually diminished in size; calyx 8 to 12 mm. long, lobes lanceolate or narrowly ovate, acute to acuminate, entirely herbaceous or narrowly scarious margined on the base; corolla 25 to 35 mm. long, 10 to 15 mm. wide, pale lavender to violet-blue, glandular externally, throat with prominent guide lines, abruptly and broadly expanded both above and below, upper lobes projecting, lower lobes spreading to reflexed, glandular and prominently bearded at the base with long whitish hairs; anther sacs explanate, as broad as long; staminode narrow, exserted, bearing a tuft of long flat, almost ribbonlike yellowish-white hairs at the tip and shorter, reflexed, golden hairs for some distance behind the tip. Figures 70, 86.

Specimens examined: NEW MEXICO. *Bernalillo County:* Forest Park, June 6, 1931, Castetter 5831 (UNM). *Colfax County:* Southwest of Capulin, June 14, 1939, *Nisbet 649* (UNM); Cimarron Canyon, July 1, 1955, *Nisbet 8667* (UNM). *Curry County:* North of Clovis, May 23, 1939, *Nisbet 1* (UNM). DeBaca County: 5 miles north of Fort Sumner, May 31, 1955, *Nisbet 1163* (UNM). *Eddy County:* Guadalupe Mountains, May 12, 1939, *Hershey* and *Nisbet 685* (UNM). *Guadalupe County:* Pastura, June 6, 1941, *Nisbet 845* (UNM). *Lincoln County:* San Patricia, June 6, 1941, *Nisbet 833* (UNM). *Mora County:* Between La Cueva and Ocate, July 2, 1955, *Nisbet 8668* (UNM). *Otero County:* Head of Alamo Canyon, Sacramento Mountains, June 7, 1941, *Nisbet 847* (UNM). *Quay County:* Near Logan, May 23, 1939, *Nisbet 648* (UNM). *Sandoval County:* Near Placitas, June 5, 1930, *Castetter 5830* (UNM). *Santa Fe County:* Junction of routes 285 and 85, June 18, 1955, *Nisbet 1164* (UNM). *San Miguel County:* 8 to 10 miles north of Las Vegas, June 18, 1955, *Nisbet 1165* (UNM). *Torrance County:* Near Gran Quivera, July 3, 1940, *Nisbet 749* (UNM). *Union County:* Breaks south of Guy, June 20, 1951, *Castetter 5836* (UNM).

Penstemon jamesii ssp. *jamesii* is a variable form as to the length of the stems, puberulence of stems and leaves, length and width of the leaves, amount of serration on the leaves, and the length and width of the corollas. On the other hand, the inflorescence is always glandular pubescent, the lower lip is always villous, and the staminode is exserted and bears the characteristic bearding. None of the above stated differences in plants east of the Rio Grande River has been found to be constant over any particular area. However, specimens from west of the Rio Grande River have consistently smaller corollas and belong to ssp. *ophianthus.*

The exact type locality of *P. jamesii* ssp. *jamesii* is not known, but it may have been in Union County. This subspecies blooms in spring and early summer on the grasslands of the plains and on open hillsides or meadows in the foothill country of southeastern Colorado, western Texas, and New Mexico east of the Rio Grande. When there is sufficient winter moisture or spring rainfall, it is exceedingly plentiful, coloring pastures and roadsides with its delicate lavender or violet-blue flowers.

30. *Penstemon jamesii* ssp. *ophianthus* (Pennell) Keck, Bull. Torr. Bot. Club 65:240. 1938.

Penstemon ophianthus Pennell, Contr. U. S. Nat. Herb. 20:343. 1920.
Penstemon pilosigulatus A. Nels., Univ. Wyo. Publ. Bot. 1:130. 1926.

Distinguished from ssp. *jamesii* by smaller corollas, 17 to 22 mm. long, 8 to 10 mm. wide; calyx 6 to 9 mm. long.

Specimens examined: ARIZONA. *Coconino County:* Near Flagstaff, June 30, 1944, *Clark 19751* (UNM); Walnut Canyon Ranger Station, June 19, 1936, *Whiting 812 B1961* (UNM). NEW MEXICO. *Catron County:* Near Pie Town, June 22, 1942, *Hershey 3522* (UNM); Wash, 4 miles southwest of Datil, August 6, 1952, *Castetter 5834* (UNM). *McKinley County:* Navajo Reservation, Nakaibito, June 1934, (UNM).

This subspecies is found west of the Rio Grande River in northern Catron County and in western Valencia, McKinley, and San Juan counties. The range extends into western Colorado, northern Arizona, and southern Utah. Some specimens from the Navajo Reservation that have been examined lacked sufficient collection data to definitely locate them, but they were collected either in northwestern McKinley County or extreme western San Juan County.

The size of the corolla seems to be the only difference between ssp. *ophianthus* and ssp. *jamesii.* The leaf characters, the shape of the corolla, and the pubescence of the staminode are identical for the two forms.

31. *Penstemon breviculus* (Keck) Nisbet and Jackson, comb. nov.
Penstemon jamesii ssp. *breviculus* Keck, Bull. Torr. Bot. Club 65:241. 1938.

Flowering stems 10 to 25 cm. tall, puberulous, solitary, few, or many on old woody rootstocks; leaves puberulous to glabrate, basal leaves elliptic, spatulate, or lanceolate, petiolate, usually acute, stem leaves lanceolate, mostly entire but occasionally with a few pointed teeth; inflorescence narrow, secund, glandular-pubescent, each peduncle bearing few to as many as 10 flowers, bracts leaflike, upper ones becoming very small; calyx 5 to 8 mm. long, lobes lanceolate, acuminate, with narrow scarious margins on the lowest one-third portions; corolla 13 to 18 mm. long, 5 to 6 mm. wide when pressed, glandular-pubescent externally, dark blue, dark violet, or blue-purple, with deep reddish purple guide lines on upper and lower throat, throat slightly to moderately inflated, the vertical diameter of the orifice as much or more than the horizontal diameter, lower lobes often overlapping and shorter than upper, the outside edges of upper and lower lobes in parallel lines, thus the face of the corolla rectangular in outline and very narrow, lower lip not glandular, bearded with long yellowish-white hairs; anther sacs small, explanate; staminode narrow, included or barely exserted, bearded with yellow almost threadlike hairs for most of the length, those at the tip long, loose, and spreading, those behind the tip much shorter, straight, and pointing backward. Figure 74.

Specimens examined: COLORADO. *Montezuma County:* 6 miles east of Cortez, June 29, 1957, *Jackson* and *Nisbet 1133* (UNM). NEW MEXICO. *San Juan County:* Breaks east of Aztec, June 1, 1952, *Clark 16274* (UNM); 2 miles south of the Colorado-New Mexico border, route 550, June 29, 1957, *Jackson* and *Nisbet 1127* (UNM); Breaks south of Farmington, May 11, 1952, *Clark 16209* (UNM); 4 miles west of Aztec, April 15, 1940, *Castetter 5840* (UNM); Flora Vista, May 17, 1947, *Clark 14231* (UNM); Rocky hillside north of Cedar Hill, June 9, 1953, *Castetter 5035* (UNM).

Keck regarded *P. breviculus* as a subspecies of *P. jamesii* but wrote "Possibly careful field study would demonstrate that this unit is fully deserving of specific rank." After careful study in the field and of many fresh plants as well as herbarium specimens, it has been thought advisable to consider *P. breviculus* as a distinct species. The unique narrow corolla seems to have little in common with the wide corolla of *P. jamesii.* This narrowness is very notable in fresh material but not so evident in herbarium specimens. The throat, although bearded, is not glandular as in *P. jamesii* and the included or barely exserted staminode has a different bearding.

Penstemon breviculus blooms in May and June on open hillsides and in the pinon-juniper woodlands. This species appears to have a very restricted range as collections have been made only in Montezuma County, Colorado, and San Juan County, New Mexico.

32. *Penstemon albidus* Nutt., Gen. N. Amer. Pl. 2:53. 1818.

Stems 2 to 4 dm. tall, one to several, erect, puberulous; leaves scabrous-puberulous, entire or obscurely toothed, those of the base petiolate and usually tapered to both ends, those of the stem lanceolate; inflorescence glandular-pubescent, narrow, not secund, peduncles bearing several flowers, bracts tapering from an ovate base, upper ones gradually diminished in size; calyx 7 to 10 mm. long, lobes lanceolate, acuminate; corollas 15 to 22 mm. long, white or sometimes shaded with violet, glandular-pubescent without and within, throat gradually and moderately expanded, not bearded on the lower lip; anther sacs explanate; staminode narrow, not exserted, sparsely bearded at and near the tip.

Specimens examined: NEW MEXICO. *Union County:* 2 miles west of Clayton, June 11, 1941, *Mankin* and *Nisbet* 856 (UNM); 32 miles west of Clayton, June 18, 1941, *Mankin* and *Nisbet* 855 (UNM); Corrumpa Creek on route 18, May 16, 1952, *Castetter* (UNM).

Penstemon albidus is easily distinguished from *P. auriberbis* by its explanate anthers and from *P. jamesii* by the gradually expanding throat and absence of bearding at the base of the lower lobes. This species is in flower from early May to early July, depending on latitude and altitude. *Penstemon albidus* is an unusually widespread species that occurs on the prairies and plains in southern Manitoba, Saskatchewan, and Alberta and southward to Oklahoma, Texas, eastern Colorado, and northeastern New Mexico.

33. *Penstemon dasyphyllus* A. Gray, U. S. and Mex. Bound. Bot. Rpt. 112. 1859. The type was collected at Cook's Spring by Wright in 1859.

Stems 2 to 4 dm. tall, few to several, puberulous; leaves linear, tapering to a sharp point, 4 to 12 cm. long, densely puberulous to glabrate; inflorescence glandular-pubescent, usually secund, peduncles one-flowered, erect, sometimes elongated; calyx 4 to 7 mm. long, lobes ovate to lanceolate, acute to short acuminate, with narrow scarious margins on the basal portion or completely herbaceous;

corolla blue or purplish blue, 25 to 35 mm. long, 9 or 10 mm. wide, lower lobes longer than the upper; anther sacs deep, completely dehiscent, not explanate, spinescent on the edges; staminode not dilated, glabrous.

Specimens examined: ARIZONA. *Cochise County:* Half a mile west of Dragoon, April 29, 1940, *Turner* and *Nisbet 698* (UNM). NEW MEXICO. *Hidalgo County:* Big Hatchet Mountains, August 18, 1954, *Castetter* (UNM). *Luna County:* Simpson Ranch, July, 1941, *Hershey 3512* (UNM).

Penstemon dasyphyllus grows on open gravelly slopes in the desert grasslands of southwestern Texas, southwestern New Mexico, southeastern Arizona, and the states of Sonora and Chihuahua in Mexico. "Cook's Spring," which is given as a type locality, is in northern Luna County.

34. *Penstemon gracilis* Nutt., Gen. N. Amer. Pl. 2:52. 1818.

Penstemon pubescens gracilis A. Gray, Proc. Amer. Acad. Arts and Sci. 6:69. 1862-63.

Stems 2 to 5 dm. tall, solitary or few, slender, puberulous; leaves glabrous or puberulous, sharply serrate or sometimes the teeth obscure, stem leaves linear or lanceolate, acute or acuminate, basal leaves short-petiolate, mostly wider than the stem leaves; inflorescence glandular-pubescent, not secund, peduncles erect, usually bearing several flowers; calyx 4 to 5 mm. long, lobes ovate, acute, narrowly scarious margined or completely herbaceous; corolla 15 to 20 mm. long, pale violet-blue, throat narrow, flattened, strongly two-ridged ventrally, lower lobes longer than the upper, bearded at the base; anther sacs narrow, not explanate, denticulate on the edges; staminode somewhat dilated, bearded for most of its length with deep yellow hairs. Figure 71.

Specimens examined: OKLAHOMA. North of Wellston, May 15, 1950, *Clark 15148* (UNM); Northeast of Oklahoma City, May 23, 1943, *Clark 10833a* (UNM). NEW MEXICO. *Colfax County:* Mountains west of Springer, Adam's Sawmill, June 18, 1939, *Nisbet 18* (UNM). *San Miguel County:* Beulah, *Porter* (NMC). *Union County:* Sierra Grande, July 30, 1940 *Nisbet 776* (UNM).

The blooming period of *P. gracilis* is in June and early July for New Mexican plants. Its range is large with northern limits in Alberta and Saskatchewan, southern limits in New Mexico, and eastern limits in Wisconsin. It grows in sandy or gravelly soil on the plains and prairies in the northern part of its range, but in Colorado and New Mexico it is found in the lower mountains associated with yellow pine. *Penstemon gracilis* is not at all common in New Mexico and only a few collections of it have been made in the northeastern part of the state.

35. *Penstemon oliganthus* Woot. and Standl., Contr. U. S. Nat. Herb. 16:172. 1913. The type was collected in the mountains west of Grants, Valencia County, August 1, 1892, by Wooton.

Stems 1.5 to 6 dm. tall from a basal rosette, solitary to several, slender, erect, puberulous; basal leaves ovate, elliptic or lanceolate, obtuse or acute, petiolate, cauline leaves two to four pairs, lanceolate or sometimes linear, glabrous or puberulous, mostly erect and shorter than the internodes; inflorescence glandular-pubescent, usually few-flowered, peduncles and pedicels erect and often elongated, bracts much reduced in size; calyx 4 to 6 mm. long, lobes lance-ovate to lanceolate, acute to acuminate, margins scarious; corolla 15 to 26 mm. long, glandular externally, blue or the upper throat reddish purple, much paler on the strongly two-ridged lower throat, bearded at the base of the lower lobes, lower lip exceeding upper by 3 to 5 mm.; anther sacs narrow, completely dehiscent, not explanate; staminode densely bearded with yellow hairs. Figures 72, 87.

Specimens examined: NEW MEXICO. *Bernalillo County:* Sandia Mountains, Sulphur Canyon, June 28, 1930, *Castetter 5849* (UNM); Sandia Crest, July 18, 1939, *Nisbet 22* (UNM). *Colfax County:* Cimarron Canyon, July 1, 1955, *Nisbet 8666* (UNM); Merino Valley, August 9, 1941, *Nisbet 866* (UNM). *Socorro County:* Hop Canyon, Magdalena Mountains, July 6, 1940, *Nisbet 758* (UNM); Mount Withington, San Mateo Mountains, July 11, 1952, *Nisbet 760* (UNM). *Taos County:* Top of Taos Pass, August 3, 1941, *Nisbet 861* (UNM). *Torrance County:* Capillo Peak, Manzano Mountains, July 3, 1953, *Castetter 2353* (UNM). *Valencia County:* Mount Taylor, July 9, 1932, *Nelson 5848* (UNM).

Penstemon oliganthus blooms from late June to August in grassy meadows or on rocky hillsides in the open pine woods and associated with spruce and fir at higher altitudes. It occurs in central Colorado southward to central New Mexico and westward to eastern Arizona.

36. *Penstemon auriberbis* Pennell, Contr. U. S. Nat. Herb. 20:339. 1920.

Stems 1 to 3.5 dm. tall, erect, solitary or several, puberulous; all leaves narrow, upper ones usually somewhat wider than the petiolate basal leaves, those of the stems 4 to 10 cm. long, entire or sometimes undulately toothed, puberulous or glabrate; inflorescence narrow, densely glandular-pubescent, bracts leaflike, lower ones wider than the leaves, acuminate; calyx 7 to 9 mm. long, lobes lanceolate, long acuminate; corolla 18 to 25 mm. long, 7 to 8 mm. wide when pressed, pale lavender to purplish blue, glandular without but not within, throat moderately to widely expanded, lobes spreading, lower ones lightly bearded at the base; anther sacs opposite, opening almost throughout, not explanate; staminode more or less exserted, somewhat dilated, densely bearded for most of the length with deep yellow hairs.

Specimens examined: COLORADO. *Pueblo County:* South of Pueblo, June 5, 1956, *Nisbet 1167* (UNM). NEW MEXICO. *Union County:* Emory Gap, north of Folsom, May 28, 1940, *Nisbet 712* (UNM).

Penstemon auriberbis flowers in late May and early June on sagebrush slopes in the foothills or on the high plains not far from the mountains. Its range is restricted to east central Colorado and southward to northern Union County, New Mexico.

37. *Penstemon rydbergii* A. Nels., Bull. Torr. Bot. Club 25:281. 1898.

Penstemon erosus Rydb., Bull. Torr. Bot. Club 28:28. 1901.
Penstemon lacerellus Greene, Leaflets 1:161. 1906.

Stems 2 to 7 dm. tall and of two kinds: long slender flowering stems, and short leafy sterile shoots arising from horizontal rootstocks, glabrous or puberulous in lines; basal leaves and those on the sterile shoots oblong or oblanceolate, obtuse or acute, glabrous, flowering stem leaves few, oblong to lanceolate, acute, glabrous; inflorescence interrupted, composed of two or more (one in depauperate plants) many-flowered fascicles, the lower one usually distant and subtended by leaflike bracts; calyx 4 to 5 mm. long, lobes linear, acuminate, the scarious and erose margins conspicuously broad; corolla 10 to 14 mm. long, bright blue to deep violet-blue, glabrous externally, strongly pubescent with yellow hairs at the base of the lower lobes, throat narrow or slightly expanded; anther sacs opposite, completely dehiscent, not explanate; staminode narrow, yellow bearded at the tip. Figure 88.

Specimens examined: NEW MEXICO. *Colfax County:* Upper Merino Valley, August 9, 1941, *Nisbet 863* (UNM); 3 miles northeast of Red River Pass, August 28, 1955, *Nisbet 1168* (UNM). *Sandoval County:* Valle Grande, Jemez Mountains, August 18, 1931, *Castetter 5864* (UNM). *San Juan County:* Washington Pass, Chuska Mountains, July 16, 1935 (UNM). *Taos County:* Meadows, upper Taos Canyon, August 3, 1941, *Nisbet 860* (UNM).

Penstemon rybergii blooms in July and August in moist meadows, aspen groves, or on gentle moist slopes of the mountains 8000 feet or higher. It occurs in the mountains of southwestern Wyoming and southward on both continental divide slopes through Colorado to northern New Mexico. The plants commonly grow in compact colonies forming very attractive masses of color.

38. *Penstemon alpinus* ssp. *brandegeei* Penland, Man. Pl. Colo. 496. 1954.

Penstemon brandegeei Porter ex Rybd. Mem. N. Y. Bot. Gard. 1:343. 1900.
Penstemon cyananthus brandegeei Porter and Coult., Syn. Fl. Colo. 91. 1874.

Stems 3 to 6 dm. tall, few to many, stout, finely puberulous below and in the inflorescence; no basal rosette of leaves at blooming time, stem leaves moderately thick, glabrous or sometimes minutely scabrous on the edges, up to 11 cm. long and 4.5 cm. wide, longer than the internodes and appearing crowded, lower leaves lanceolate or oblanceolate with short, margined petioles, upper leaves elliptic, lanceolate, or ovate, acute at the apex, sessile or cordate at the base; inflorescence broad and compact, many-flowered, secund, peduncles and pedicels puberulous, lower bracts large, leaflike, upper ones gradually diminished in size; calyx 6 to 8 mm. long, lobes ovate or orbicular, the margins of the base broadly scarious and erose, the tip abruptly acuminate; corolla 30 to 40 mm. long, 14 to 18 mm. wide, blue, the throat often reddish purple, much expanded, glabrous or slightly pubescent on the lower lip; anther sacs completely dehiscent, not explanate, pubescent with a few short stiffish hairs, denticulate on the edges; staminode exserted, stout, dilated and usually notched at the apex, glabrous or rarely with a few hairs at the tip. Figures 81, 89.

Specimens examined: NEW MEXICO. *Colfax County:* Johnson's Mesa, July 1939, *Nisbet 17* (UNM); Breaks west of Yankee, August 8, 1951, *16134* (UNM). *Union County:* West of Grenville in railroad right of way, June 14, 1939, *Nisbet 16* (UNM).

This beautiful subspecies blooms the last half of June and through July in the lower mountains and on the high plains close to the mountains in southeastern Colorado and northeastern New Mexico. Subspecies *brandegeei* is adaptable to garden culture probably because its natural habitat is the richer, deeper soil of the valleys and high plains. However, it is also found growing on rocky hillsides.

Garden grown plants in Colfax County lived five to eight years and older plants had as many as 30 stalks. *Penstemon alpinus* ssp. *brandegeei* hybridizes with *P. alpinus* ssp. *alpinus* in southcentral Colorado where they meet. The extremes of the two entities differ considerably, but many intermediate plants have been collected.

39. *Penstemon strictus* Benth. ssp. *strictus,* DC. Prod. 10:324. 1846.

Stems 2 to 8 dm. tall, glabrous, one to several from a woody rootstock; basal leaves spatulate, usually with long petioles, stem leaves 4 to 12 cm. long, linear to broadly lanceolate, glabrous; inflorescence narrow, secund, peduncles and pedicels short or the lower ones somewhat elongated but erect; calyx 3 to 6 mm. long, lobes ovate to lanceolate, acute, margins narrowly or widely scarious; corolla 18 to 28 mm. long, dark blue or violet-blue, prominently bilabiate, throat moderately expanded above and below, lower lobes longer than the upper ones and occasionally lightly bearded at the base; anther sacs opposite, completely dehiscent, not explanate, lightly to heavily bearded with long, soft, white hairs, denticulate on the edges; staminode glabrous or with a few short hairs on the somewhat dilated tip. Figures 73, 77, 90.

Specimens examined: COLORADO. *Montezuma County:* 6 miles east of Mancos, June 29, 1957, *Jackson* and *Nisbet 1128* (UNM). NEW MEXICO. *Bernalillo County:* Sandia Crest, July 25, 1938, *Nisbet 15* (UNM). *Colfax County:* Merino Valley, June 24, 1939, *Nisbet 11* (UNM); Near top of Red River Pass, June 28, 1939, *Nisbet 658* (UNM); *McKinley County:* Mexican Springs, July 20, 1936 (UNM, 4432). *Rio Arriba County:* Mountains, 18 miles southwest of Tres Piedras, August 8, 1955, *Nisbet 10473* (UNM); Hibben's Ranch, Rio de los Pinos, July 5, 1942, *Castetter* (UNM); Cumbres Pass, September 14, 1953, *Castetter 5877* (UNM). *Sandoval County:* Pine woods, 3 to 5 miles north of Cuba, July 8, 1948, *Castetter* and *Dittmer 5878* (UNM). *Taos County:* Tres Ritos, July 4, 1948, *Castetter* and *Dittmer 5875* (UNM); Taos side of U. S. Hill, July 2, 1955, *Nisbet 8659* (UNM). *Torrance County:* 5 miles from Capillo Peak, Manzano Mountains, July 3, 1953, *Castetter 2354* (UNM).

Penstemon strictus ssp. *strictus* is a variable species in the width of the leaves, the amount of bearding on the anthers and staminode, the length and width of the calyx lobes, and the flower size and color. Plants with linear leaves can be found growing near those with broadly lanceolate leaves, flowers of pure blue next to violet-blue blossoms, and corollas with glabrous staminodes in the same colony with those having slightly bearded staminodes. Considerable difference in the length and width of the calyx can be found on the same plant, particularly on some plants from Rio Arriba County where they are in contact with ssp. *strictiformis.*

On the Sandia Crest in Bernalillo County, plants of *P. strictus* ssp. *strictus* are very low, 1 to 2 dm. tall with declined stems, a short inflorescence, and an extensive woody root system. These variations are probably adaptations to the high altitude and exposed habitat. Another interesting plant was found by Mrs. E. L. Barrows in the mountains near Santa Fe. The flowers of this plant were a clear pink without a trace of the normal blue colo

Penstemon strictus ssp. *strictus* blooms from late June to August in open meadows, on wooded slopes, and on rocky hillsides in the yellow pine or spruce and fir woodlands.

40. *Penstemon strictus* spp. *strictiformis* (Rydb.) Keck, Jour. Wash. Acad. Sci. 29:491. 1939.

Penstemon strictiformis Rydb., Bull. Torr. Bot. Club 31:642. 1905.

Similar to *P. strictus* ssp. *strictus* except the calyx 8 to 10 mm. long, the lobes broadly ovate and acuminate, the edges of the base widely scarious and erose; corolla usually 25 to 35 mm. long, light blue to violet, throat ventricose below, almost flat above, anthers usually heavily bearded with long hairs; staminode dilated and more or less bearded. Figure 80.

Specimens examined: COLORADO. *Montezuma County:* 12 miles east of Cortez, June 29, 1955, *Jackson* and *Nisbet 1132* (UNM); Two miles west of Mancos, June 29, 1957, *Jackson and Nisbet 1138* (UNM). NEW MEXICO. *Rio Arriba County:* El Vado Lake, June 20, 1941, *Mankin* and *Nisbet 851* (UNM); Ten miles north of Regina, June 20, 1941, *Mankin* and *Nisbet 853* (UNM). *San Juan County:* Two miles south of the Colorado-New Mexico state line, north of Aztec, June 29, 1957, *Jackson* and *Nisbet 1126* (UNM).

Collections listed above (*Jackson* and *Nisbet 1138* and *1132*) were made in the type locality of *P. strictus* ssp. *strictiformis.* These specimens differ considerably from *P. strictus* ssp. *strictus.* However, many specimens from Rio Arriba County and also from Colorado are intermediate for some or all of the characteristics that distinguish the two subspecies. Subspecies *strictiformis* occurs in southwestern Colorado, northwestern New Mexico, and perhaps in northeastern Arizona and adjacent Utah. It is found in the same type of habitat as ssp. *strictus.*

41. *Penstemon virgatus* A. Gray, U. S. and Mex. Bound. Bot. Rpt. 113. 1859. The type was collected near Santa Rita by Bigelow and Wright in 1851.

Stems 2.5 to 8 dm. tall, puberulous or glabrate, slender, solitary or few; leaves linear or narrowly lanceolate, 2 to 12 cm. long, 2 to 6 mm. wide, glabrous or puberulous; inflorescence narrow, secund, sometimes short but usually elongated, peduncles short, erect, with one to five flowers; calyx 3 to 4 mm. long, lobes ovate, elliptic, or obovate, tips acute, short acuminate, obtuse, or occasionally truncate with a mucro, margins scarious and more or less erose; corolla 15 to 24 mm. long, glabrous externally, pale violet, violet-blue, white, or rarely pink, usually strongly marked with red-purple guide lines, prominently bilabiate, throat abruptly and broadly expanded above and below, upper lobes projecting or spreading, lower ones spreading or reflexed, glabrous or lightly pubescent on the lower lip; anther sacs oblong, completely dehiscent, not explanate; staminode narrow or moderately dilated, glabrous. Figures 75, 76.

Specimens examined: ARIZONA. *Apache County:* 3 to 5 miles southwest of Showlow, June 26, 1957, *Nisbet 1145* (UNM). *Yavapai County:* Mogollon Rim, September 2, 1956, *Nisbet 1020* (UNM). NEW MEXICO. *Bernalillo County:* Forest Park, Sandia Mountains, June 20, 1940, *Nisbet 741* (UNM); Cedro Canyon, 25 miles southeast of Albuquerque (pink flowers) July 3, 1940, *Nisbet 753* (UNM). *Colfax County:* Merino Valley, August 15, 1956, *Nisbet 1141, 1143* (UNM). *Catron County:* Willow Creek Campground, August 9, 1952, *Castetter 5902* (UNM); West of Datil, July 16, 1944, *Hershey 3190* (UNM). *Grant County:* Santa Rita Mountains, October 9, 1904, *Metcalf 1466* (UNM). *Lincoln County:* Gallina Mountains, July 29, 1950, *Clark 15962* (UNM). *Sandoval County:* Bandelier National Monument, August 3, 1941, *Nisbet 857* (UNM). *Taos County:* 3 miles south of Tres Piedras, August 8, 1955, *Nisbet 1170* (UNM); Penasco, foot of U. S. Hill, July 3, 1939, *Nisbet 7* (UNM). *Torrance County:* 15 miles south of Mountainair, July 3, 1940, *Nisbet 755* (UNM). *Valencia County:* Near Paxton Springs, August 8, 1954, *Castetter* (UNM).

Penstemon virgatus is extremely variable as to the color and size of the flowers, the amount and location of the puberulence, and the size and shape of the calyx lobes. In the type locality the corollas are usually violet-blue and large for the species. The puberulence may be confined to the lower stem and leaves or may extend to the stem, peduncles, and pedicels of the inflorescence. Occasionally plants may be almost completely glabrous. This is particularly true in Colfax County where the species comes into close contact with *P. unilateralis* Rydb. of the Colorado Mountains, and in Northern Lincoln County where its range nears that of *P. neomexicanus* Woot. and Standl. *P. virgatus* ssp. *arizonicus* (A. Gray) Keck, found in the White and Graham mountains of Arizona, has a bearded staminode, oblong-spatulate leaves, and broadly scarious and erose margined calyx lobes. One or more of these characteristics are frequently seen in plants from western New Mexico. Colonies of the form with white corollas are not uncommon while plants with pink corollas occur only rarely. *Penstemon virgatus* blooms from June to September in the mountains of central and eastcentral Arizona and westcentral, central, and northcentral New Mexico.

42. *Penstemon neomexicanus* Woot. and Standl., Contr. U. S. Nat. Herb. 16:172. 1913. The type was collected in pine woods on Eagle Creek in the White Mountains, August 15, 1907, by Wooton and Standley.

Stems 4 to 7 dm. tall, solitary or several, glabrous, slender or often stout; basal leaves lanceolate or oblanceolate with margined petioles, often absent on flowering plants, stem leaves lanceolate or occasionally linear, 6 to 18 mm. wide, glabrous; inflorescence usually elongated and many-flowered, secund, not crowded, lower peduncles and pedicels sometimes elongated, lower bracts leaflike; calyx 4 to 7 mm. long, lobes obovate or oblong, obtuse or truncate with a short mucro (rarely acute), margins scarious and erose; corolla 26 to 35 mm. long, blue, blue-purple, or violet-blue, throat broadly expanded, 10 to 17 mm. wide when pressed, lobes spreading, base of lower lobes usually strongly bearded; anther sacs oblong, completely dehiscent, not explanate; staminode glabrous, much dilated, often notched at the tip. Figures 78, 79.

Specimens examined: NEW MEXICO. *Lincoln County:* Two miles west of Capitan, August 14, 1952, *Castetter 5896* (UNM); Nogal Lake, July 3, 1940, *Nisbet 765* (UNM); Capitan Pass, northeast of Capitan, July 5, 1940, *Nisbet 748* (UNM); Pine Lodge, Capítan Mountains, August 16, 1952, *Castetter 5898* (UNM); South Fork of Little Eagle Creek, July 4, 1940, *Nisbet 768* (UNM); Two miles above Bonita Dam, August 18, 1949, *Gordon* and *Dunn 774* (UNM). *Otero County:* Cloudcroft, August 5, 1939, *Hershey* and *Nisbet 677* (UNM); 5.6 miles northwest of Mayhill, August 13, 1949, *Gordon* and *Norris 574* (UNM); Karr Canyon, Sacramento Mountains, August 3, 1952, *Castetter 5897* (UNM).

Penstemon neomexicanus occurs in the Capitan, White, and Sacramento mountains of Lincoln and Otero counties. This species blooms in July and August on wooded slopes and in open glades of the pine woodlands and at higher elevations among the spruce and fir.

There is some evidence that *P. neomexicanus* hybridizes with *P. virgatus.* Some plants collected in northern Lincoln County may be considered intermediate between the two species. An effort has been made recently to find hybrids of these two species, but due to the drought of the past several years, vegetation in the area concerned has been very sparse. No collections have been made from southern Torrance County and northern Lincoln County for a number of years. The larger and more brightly colored corollas, the looser inflorescence, and the wider leaves of *P. neomexicanus* give it a very different appearance from *P. virgatus. Penstemon unilateralis* of Colorado is closely allied with *P. neomexicanus* and *P. virgatus. Penstemon neomexicanus* has considerably larger corollas than either *P. virgatus* or *P. unilateralis*, but in leaf characters and lack of puberulence it closely resembles *P. unilateralis. Penstemon virgatus*, as found in the Merino Valley of Colfax County in northcentral New Mexico, is probably a hybrid form since some of these plants exhibit the characteristics which distinguish *P. unilateralis* from *P. virgatus.* Until more experimental evidence can be gathered on this group of closely related species, it was thought best to retain each as a species.

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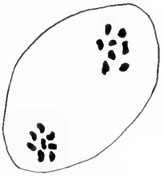
FIGURES 1-16

FIGS. 1-16. Chromosomes of certain species of *Penstemon.*

FIG. 1. *P. alamosensis*—telophase I.
FIG. 2. *P. alpinus* ssp. *brandegeei*—diakinesis.
FIG. 3. *P. ambiguus* ssp. *ambiguus*—diakinesis.
FIG. 4. *P. angustifolius* ssp. *caudatus*—diakinesis.
FIG. 5. *P. barbatus* ssp. *torryi*—prophase of mitosis.
FIG. 6. *P. crandallii* ssp. *glabrescens*—anaphase I.
FIG. 7. *P. crandallii* ssp. *glabrescens* var. *taosensis*—mitotic metaphase.
FIG. 8. *P. cardinalis* ssp. *cardinalis*—diakinesis.
FIG. 9. *P. eatonii* ssp. *exertus*—diakinesis.
FIG. 10. *P. jamesii* ssp. *jamesii*—metaphase I.
FIG. 11. *P. linarioides* ssp. *coloradoensis*—diakinesis.
FIG. 12. *P. neomexicanus*—anaphase II.
FIG. 13. *P. oliganthus*—telophase II.
FIG. 14. *P. ovatus*—late diakinesis.
FIG. 15. *P. parryi*—metaphase I.
FIG. 16. *P. pinifolius*—diakinesis.

FIGURES 1-16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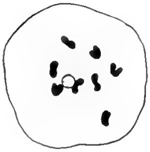
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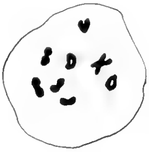
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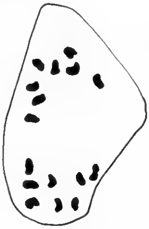
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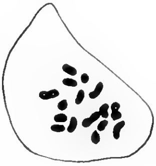
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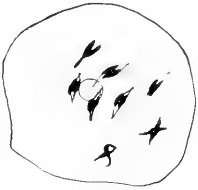
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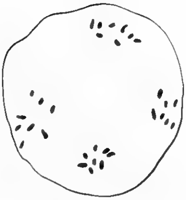
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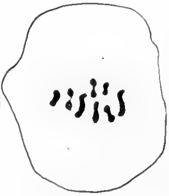
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FIGURES 17-23

FIGS. 17-23. Chromosomes of certain species of *Penstemon.*

FIG. 17. *P. psuedospectabilis* ssp. *connatifolius*—metaphase I.
FIG. 18. *P. secundiflorus*—telophase I.
FIG. 19. *P. strictus* ssp. *strictus*—anaphase II.
FIG. 20. *P. thurberi*—telophase II.
FIG. 21. *P. unilateralis*—diakinesis.
FIG. 22. *P. virgatus*—diakinesis.
FIG. 23. *P. whippleanus*—diakinesis.

Figures 17-23

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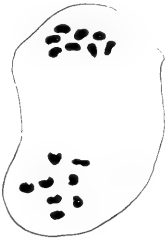

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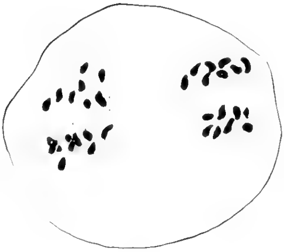

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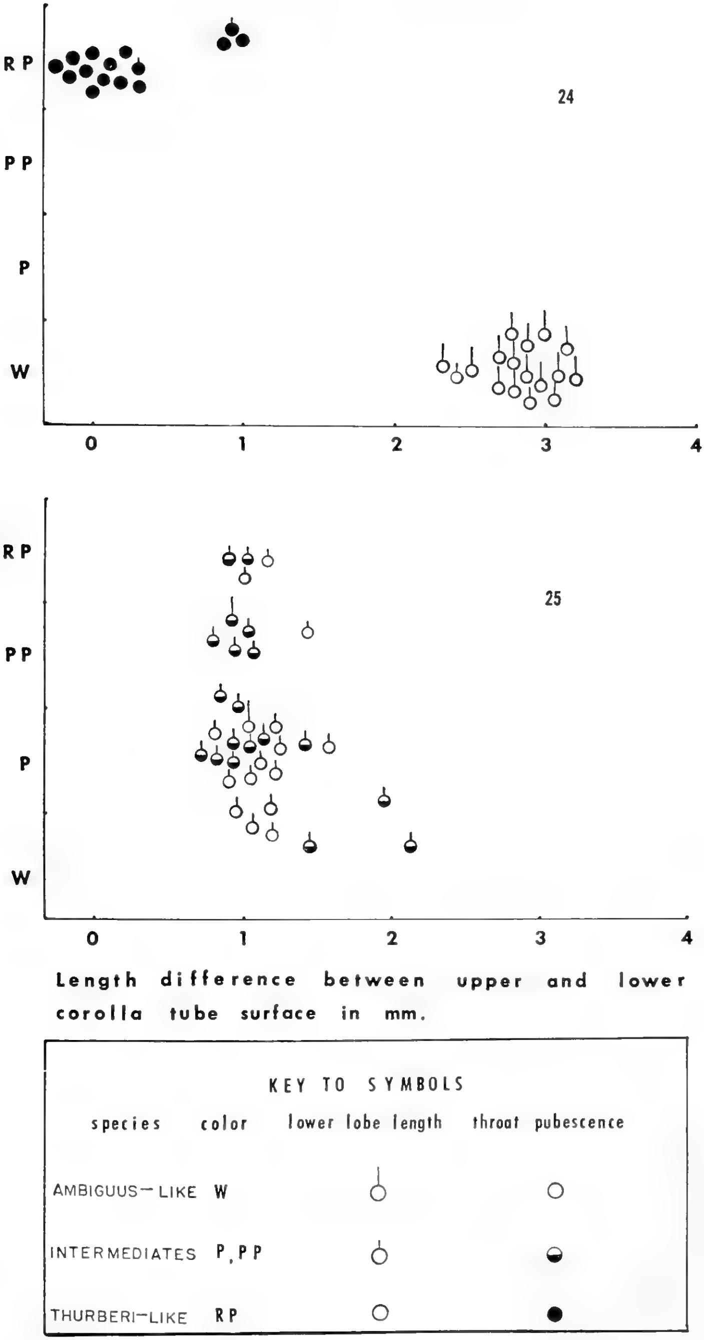
FIGURES 24 AND 25

FIG. 24. Scatter diagram of *Penstemon ambiguus* in lower right and *P. thurberi* in upper left corner.

FIG. 25. Scatter diagram of putative hybrids between *P. ambiguus* and *P. thurberi*.

FIGURES 24 AND 25



FIGURES 26-41

FIGS. 26-28. *Penstemon pinifolius*—26, corrolla; 27, habit; 28, staminode.

FIGS. 29-31. *P. pseudospectabilis* ssp. *connatifolius*—29, connate-perfoliate leaf; 30, corolla; 31, explanate anther.

FIGS. 32, 33, 36. *P. cardinalis* ssp. *cardinalis*—32, corolla; 33, calyx lobe; 36, median stem leaf.

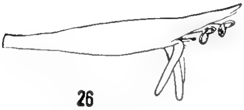
FIGS. 34-35. *P. cardinalis* ssp. *regalis*—34, calyx lobe; 35, median stem leaf

FIGS. 37-38. *P. bridgesii*—37, saccate anther; 38, side view of saccate anther.

FIGS. 39-40. *P. superbus*—39, corolla; 40, face of corolla showing almost regular arrangement of lobes.

FIG. 41. *P. alamosensis*—corolla.

Figures 26-41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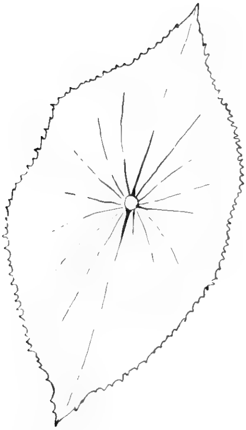
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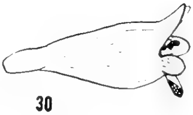
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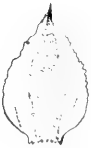
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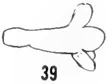
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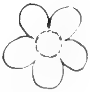
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FIGURES 42-61

FIGS. 42, 44. *P. superbus*—42, median stem leaf; 44, staminode.

FIGS. 43, 45. *P. alamosensis*—43, median stem leaf; 45, staminode.

FIG. 46. *P. lanceolatus*—anther.

FIG. 47. *P. eatonii*—anther.

FIG. 48. *P. barbatus* ssp. *trichander*—anther.

FIG. 49. *P. barbatus* ssp. *barbatus*—corolla.

FIGS. 50-51. *P. buckleyi*—50, bract; 51, bract.

FIG. 52. *P. angustifolius* ssp. *caudatus*—bract.

FIGS. 53, 55. *P. secundiflorus*—53, bud; 55, habit.

FIGS. 54, 56. *P. fendleri*—54, bud; 56, habit.

FIGS. 57, 59. *P. ambiguus* ssp. *ambiguus*—57, corolla; 58, corolla face; 59, bud.

FIGS. 60-61. *P. thurberi*—60, corolla; 61, corolla face.

FIGURES 42-61


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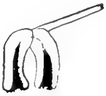
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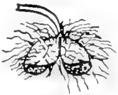
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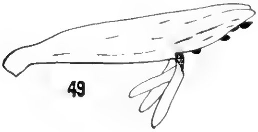
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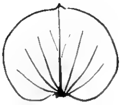
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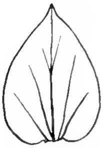
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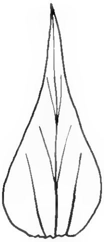
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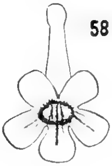
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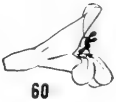
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FIGURES 62-81

FIGS. 62-64. *P. linarioides* ssp. *linarioides*—62, corolla; 63, staminode; 64, calyx lobe.

FIG. 65. *P. linarioides* ssp. *coloradoensis*—staminode.

FIGS. 66-68. *P. crandallii* ssp. *glabrescens*—66, calyx lobe; 67, staminode; 68, corolla.

FIG. 69. *P. whippleanus*—corolla.

FIG. 70. *P. jamesii* ssp. *jamesii*—corolla.

FIG. 71. *P. gracilis*—median stem leaf.

FIG. 72. *P. oliganthus*—median stem leaf.

FIGS. 73, 77. *P. strictus* ssp. *strictus*—73, anther; 77, corolla.

FIG. 74. *P. breviculus*—corolla.

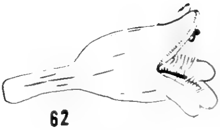
FIGS. 75-76. *P. virgatus*—75, corolla; 76, staminode.

FIGS. 78-79. *P. neomexicanus*—78, corolla; 79, staminode.

FIG. 80. *P. strictus* ssp. *strictiformis*—corolla.

FIG. 81. *P. alpinus* ssp. *brandegeei*—staminode.

FIGURES 62-81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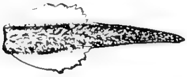
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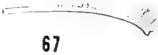
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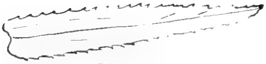
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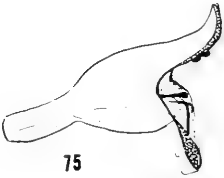
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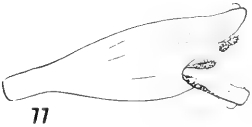
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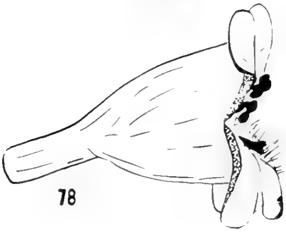
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FIGURES 82-90

FIGS. 82-90. Habit and type of inflorescence of certain species of *Penstemon*.
FIG. 82. *P. superbus.*
FIG. 83. *P. barbatus* ssp. *torreyi.*
FIG. 84. *P. secundiflorus.*
FIG. 85. *P. crandallii* ssp. *glabrescens.*
FIG. 86. *P. jamesii* ssp. *jamesii.*
FIG. 87. *P. oliganthus.*
FIG. 88. *P. rydbergii.*
FIG. 89. *P. alpinus* ssp. *brandegeei.*
FIG. 90. *P. strictus* ssp. *strictus.*

FIGURES 82-90


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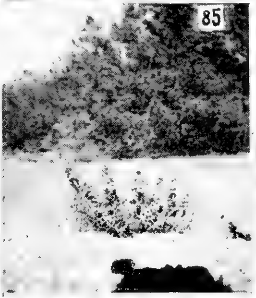
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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLI] December 23, 1960 [No. 6

The Biology of *Nomia (Epinomia) triangulifera* With Comparative Notes on Other Species of *Nomia*[1]

BY

Earle A. Cross [2] and George E. Bohart [3]

Abstract: Observations on the biology and early stages of *Nomia (Epinomia) triangulifera* Vachal, *N. (E.) nevadensis arizonensis* Ckll., *N. (Dieunomia) heteropoda* (Say), and *N. (Acunomia) melanderi* Ckll. show that the subgenera *Epinomia* and *Dieunomia* are more closely related to each other than either is to *Acunomia*. Although *nevadensis* closely resembles *triangulifera* in many particulars, its brood cells, eggs, and developing larvae are somewhat intermediate between those of *triangulifera* and *melanderi*. In the same characteristics *heteropoda* is more like *triangulifera*, indicating that the relation between *Dieunomia* and *Epinomia* is better expressed by *triangulifera* than by *nevadensis*.

In contrast with the one species of *Acunomia*, the two species of *Epinomia* and the one of *Dieunomia* hold in common the following characteristics:

1. Flight period in August and September instead of July and August.
2. Host plants nearly limited to Compositae.
3. Tumulus with a lateral plugged entrance and a horizontal vestibule.
4. Brood cells pendant in series from one or two nearly straight, horizontal laterals.
5. Narrowly oval cells with conical and not obviously spiraled ceilings.
6. Pollen balls less convex above than below and with an equatorial flange.
7. Early stage larvae with lobate ventrolateral projections of the body segments.

N. (Epinomia) nevadensis approaches *melanderi* in having moderately long, well-arched eggs, a relatively shallow nest, and slightly more oval cells than the other two species.

All four species nest in soil that is low in organic material, sparsely vegetated, and damp nearly to the surface.

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INTRODUCTION

In a recent paper Cross (1958) redefined the taxonomic status of the genus *Nomia* Latreille on morphological grounds. He grouped the North American members of the genus into four subgenera: *Paranomina* Michener, *Acunomia* Cockerell, *Epinomia* Ashmead, and *Dieunomia* Cockerell. These were placed in two distinct units, the first composed of *Acunomia* and *Paranomina,* and the second *Epinomia* and *Dieunomia.* The following observations on the biologies of a limited number of species involving three of the four subgenera appear to support these groupings. In Table 1 a comparison is made of similarities and differences among the three subgenera based on studies conducted in Kansas and Utah in 1954, 1955, and 1959.[4]

Published information on the biology of *Nomia* is scanty, the most extensive papers being those on *N. (Acunomia) melanderi* Ckll. by W. P. Stephen (1959), G. E. Bohart (1947, 1950, 1952, 1959), and Bohart and Cross (1955). Information on species of *Paranomina* is limited to several observations by Cockerell (1934). The same is true of *Dieunomia* (Blair, 1935). More extensive papers by Pierce (1904) and Rau (1929) have summarized our knowledge of *N. (Epinomia) triangulifera* Vachal. Hicks (1926) and Cockerell (1898, 1934) have published short notes on the habits of *N. (Epinomia) nevadensis bakeri* Cockerell.

This paper deals primarily with studies of *N. triangulifera.* However, several nests of *N. (Epinomia) nevadensis arizonensis* Cockerell and one nest of *N. (Dieunomia) heteropoda* (Say) were examined and are discussed herein. A detailed study of *N. melanderi* will be published elsewhere, but a few features of its biology are brought out in the following discussion for purposes of comparison.

Nomia triangulifera Vachal

This medium-sized, black bee (Fig. 1) is distributed throughout the central United States from central Illinois and Minnesota westward to Utah and southern New Mexico. It is a gregarious species, often establishing many thousands of nests in a single site (Fig. 2).

NESTING SITES.—The nesting habits of this species were studied at the eight sites described below:

1. Five miles northwest of Lawrence, Kansas. The bees were nesting in great numbers on an alluvial sand deposit which resulted from the 1951 flooding of the Kansas River. The deposit occupies what was formerly an ox-bow lake of the river. The

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[4] In Kansas by Cross; in Utah by Cross and Bohart.

area is now a rolling sandy waste, populated by scattered clumps of cottonwoods and invader annuals such as *Euphorbia hexagona, Helianthus annuus,* and *Cenchrus pauciflorus.* The sand deposits on the silt bed of the old lake are from 3 to 11 feet deep and are broken by innumerable thin, irregularly spaced strata of silt (none over 30 cm. deep). Probably because of the underlying silt bed, the sand holds its moisture fairly well below a depth of a foot or so, and at the level of the cells it is moist enough to pack.

2. A pasture two miles north of Topaz, Utah. This site occupies the slope of a borrow pit and is sub-irrigated, apparently from an adjacent canal. The top layer of soil to a depth of 21 cm. is a sandy loam, beneath which is a silt loam interspersed with narrow zones of clay loam. Vegetation is sparse but uniform over the entire site and consists of a cover of salt grass (*Distichlis stricta*). *N. triangulifera* shares some of the more moist portions of this site with the alkali bee, *N. melanderi.*

3. A series of alkaline mounds in an area with high artesian pressure near the Logan-Cache Airport in Cache Valley, Utah. The soil is a loam with moisture seeping upward to the surface throughout the season. On some of these mounds *N. triangulifera* occupies space with *N. melanderi.*

4. A steep road bank near Myton, Utah, with an eastern exposure. The surface is nearly bare and the soil ranges from a loam to a sandy loam except for scattered large rocks. Moisture is evident during dry weather below a vertical depth of about three inches.

5. A race track at Hinckley, Utah. The sandy soil on the track surface is underlain with a silt loam at a depth of three to five inches.

6. An alkali flat five miles west of Smithfield, Utah. The fine silt loam soil is nearly saturated with moisture during the nesting season.

7. A large, bare, clay loam slope in Pleasant Valley, Uinta Basin, Utah. On this site even the lightest rainfall fails to soak in.

8. A series of low sand dunes, some stabilized and some still slowly shifting, near Cornish, Utah. The soil is composed of almost pure sand with a zone of moderate compaction in the stabilized areas from one to two feet deep. The soil is completely dry for several inches and scarcely moist enough even at three feet to hold together when compressed in the hand.

Pierce (1904) and Rau (1929) found nests in heavy clay soils, and C. D. Michener (unpublished) observed a site near Colby, Kansas, in hard heavy soil cleared of vegetation by occasional vehicular traffic.

From the foregoing, it is apparent that *triangulifera* nests in soils with a wide range of moisture and texture. In physical type, the soils include sand, sandy loam, loam, silt loam, and clay loam. The mechanical composition of several sites in Utah is shown in Table 2. An absence of crumb structure in the natural state and a low organic content are common to all sites observed. Appreciable moisture can always be found at deeper levels from 30 to 60 cm. and some sites are nearly saturated up to the surface, even in dry weather. Nevertheless, preference is always for areas well drained at the surface. The bees usually occupy knolls or gentle slopes, but in sandy washes or hard-packed clays they may choose level ground. The sites may be entirely bare or have sparse herbaceous growth, but the ground is never densely shaded.

In general, *triangulifera* seems to use the same criteria as *melanderi* for choosing its sites. However, it is less particular about moisture conditions at the surface and, unlike the latter, will nest in areas with several inches of loose, dry surface soil. In sites like the one at Topaz, where only the top layers of soil are sandy, the cells are always placed in a layer containing more silt or clay. The location of finer layers of soil, as well as moisture and temperature factors, seems to play a part in determining the depth of the brood cells. The deepest nests (2½ feet) were found at Cornish, Utah, where moisture was low and the sand was easy to excavate. The shallowest nests (11-14 inches) were found at Myton, Utah, where rocks and shaly spots were numerous at greater depths.

LIFE CYCLE.—*Diapause.* Like all species of *Nomia* studied, *triangulifera* overwinters as a prepupa in a rigid and motionless state of diapause in which it can resist strong mechanical shocks, pressures, and fluctuations in temperature and humidity.

The prepupa of *triangulifera* is readily distinguished from that of *melanderi* by the sharper dorsal prominences on the thorax (Fig. 3). The integument is somewhat more rigid, and laboratory studies show it to be more subject to desiccation. Its color is usually butter-yellow with intersegmental bands of orange, especially dorsally on the thorax. For reasons discussed later it is sometimes white. *N. melanderi* prepupae, which are always white, have a slightly greyish tinge in contrast to the more opaque color of *triangulifera*.

Studies in progress at Utah and California on factors initiating the breaking of diapause in several species of ground-nesting bees, including *N. triangulifera, melanderi,* and *nevadensis,* indicate that if the prepupae are held for 10 days or more at 75° F. and then incubated at 80° to 85° F., at least a few individuals will break diapause. However, a cold period prior to incubation assists diapause breaking. Work now in progress indicates that the longer the cold period (up to at least 120 days), the more rapid and complete is the breaking of diapause after the temperature is raised. Under natural conditions, the winter provides a sufficiently cold period of several months. Following this, the temperatures at the cell level are still too cool for diapause to break until late in June or July. At Topaz, Utah, all *triangulifera* in the nesting site were still in the prepupal stage on July 6, 1956, but a few showed signs of breaking diapause.

Visible signs of the termination of diapause consist of a slight softening of the body wall and a less pronounced angle between the thorax and abdomen. This stage is known as the propupa and begins with the actual molting to the pupal stage within the prepupal skin. During this period the bee exhibits faint response to external stimuli and makes occasional, almost imperceptible, flexing movements. Because the signs of this stage appear gradually, its duration is not certain, but in most cases it appears to last from two to four days.

Shedding of the prepupal skin. For several hours before shedding its skin, the insect increases its flexing movements and also makes a few slight rotating movements with its posterior end. Shedding of the larval skin by normal individuals lying on a piece of cellucotton takes from one to six minutes and proceeds smoothly in the usual pattern for holometabolous insects. Injured, desiccated, or otherwise abnormal prepupae usually fail to shed their skins completely. These pupae often continue to develop within the larval skin and may become almost fully pigmented before dying. Pupae kept in the laboratory at 80° F. and 75 percent relative humidity remained in the pupal stage an average of 14 days for both sexes with a usual range of 11 to 19 days. On the average it took six days for the eyes to become dark. A few pupae remained for an unaccountably long time in an unpigmented condition (up to 20 days) and then developed at the normal rate.

The unpigmented pupa is soft and motionless, although it can rotate its posterior end slightly when disturbed. As it hardens and becomes pigmented, the rotational movements increase and flexing movements of the body take place. The white pupa, although delicate, can withstand handling and desiccation far better than after it is pigmented.

Ecdysis. For several hours before shedding its skin, the pupa increases the tempo of its rotating and flexing movements and is responsive to stimuli. The process of skin-shedding normally takes from 5 to 10 minutes. The newly emerged adult, although responsive to external stimuli, has soft, white wings and remains nearly motionless in its cell for about two days while the wings are hardening. The bee then tunnels to the surface, but does not venture forth at once. Apparently, the male takes flight within an hour, but the female usually remains in her natal burrow for at least 24 hours, spending much of this time just below the surface.

Time of emergence. Because males are more precocious about flying than females, it is difficult to determine how much sooner they develop into adults. Usually a few males appear at least a week before the first females take flight, and they are found in large numbers over the burrows during the last few days of this period. The pre-courtship flight of the males usually takes place in the first or second week of August, but in some localities and seasons, the first males are not seen until the third week.

Pre-courtship flight. Before the females begin to fly the males conduct a low, weaving flight over the nesting site and pounce on any female that shows her head above the surface. They often drop to the ground and dig at open holes or ones that have been opened and later plugged (Fig. 1). These are probably burrows containing females still too immature to venture forth. This activity by the males suggests that they respond to an odor produced by the young females.

Mating. When the females leave their burrows, they are at once seized by males. In this species, the female often resists the attentions of the male and many mating attempts result in short struggles ending with the escape of the female. Apparently, copulation rarely or never takes place during such encounters. Four examples of a definite courtship pattern, unlike any we have seen in other solitary bees, were noticed at the Lawrence and Topaz sites. Observation of a mating pair, beginning with actual copulation, was made on the window ledge of a greenhouse at Logan, Utah.

At the start of the courtship the female rests quietly on the ground and does not attempt to avoid the attentions of the male. The latter crawls upon her back and locks his forelegs beneath her mesothorax and his midlegs between her fore and hind wings and under her propodeum. His hind legs lock beneath the posterior portion of her abdomen. During courtship and copulation the female extends her forewings slightly upward and outward, thus forming a sort of "cradle" for the thorax of the male. A type of "mating dance," best described in two phases, is then performed by the male as follows:

1. He pulsates his abdomen rapidly and rhythmically, accompanying this with alternate vertical and lateral jerking of the antennae.
2. He flutters his wings, at the same time drumming his abdomen rapidly against that of the female.

These two phases alternate and last a few seconds each. The dance lasts several minutes, during which time the female remains passive and the male makes one or more mating attempts. Copulation ultimately takes place when the male slides posteriorly, reaching forward and slightly upward with the tip of his abdomen to contact the female. Actual copulation was seen to last from eight seconds to slightly more than one minute. During copulation the male strokes the female with his antennae at a rate of about one stroke per second.

Full courtship and mating were infrequently observed, which may indicate that the complete pattern is not always followed or that it sometimes occurs away from the nesting site. Males are common on *Helianthus* flowers and were observed there several times trying to mate without preliminary courtship.

Nesting period. Collection records of females give a good indication of the duration of the nesting period. Examination of 148 female specimens in collections made between 1890 and 1959 from all parts of the range showed that nearly all were taken between August 10 and September 15, but one was taken as late as October 2 (Lincoln, Nebraska). The few specimens available from the southern portions of the range did not indicate earlier emergence in such areas. Likewise, Cockerell (1898) records males and females at Las Cruces, New Mexico, on September 11 and 14. Considering that emergence of females continues for at least two weeks, as based on the appearance of new nests, and that few adults are still alive more than six weeks after the earliest emergence, it appears that the nesting period of individual females is seldom greater than one month. No evidence of a second generation has been found at any of the nesting sites, probably because the soil temperatures are too cool after mid-September for further development to take place.

In 1954 on the Lawrence site, nesting began near the middle of August. Only an occasional new nest was begun after September 18, and activity had tapered off by that time. By September 26 activity by adults had ceased. In 1958 on the Pleasant Valley, Utah site the first signs of nesting were observed on August 16. At this time there were still a few *N. melanderi* provisioning nests in the same area, but their activity had nearly ceased. On September 5, *triangulifera* activity had reached its peak and *melanderi* had disappeared. On September 23, no new nests of *triangulifera* could be found, and only a few adults still provisioning nests were seen. Several thousand fresh mounds of *melanderi*, representing a small second generation were now in evidence. On October 6, a few *melanderi* nests were still active, but no *triangulifera* adults could be found.

The coincidence between the nesting season of *triangulifera* and blooming of *Helianthus annuus* is apparently assured by the depth of the brood cells. The cells of *triangulifera* are always at least 5 to 31 cm. deeper than those of *melanderi*, where the two species nest together. Apparently, as a result of cooler temperatures at the greater depths, *triangulifera* emerges from a month to six weeks later than *melanderi*. The question arises, does the depth of the cells condition the choice of host plant or vice versa?

N. triangulifera usually starts nesting some time after *H. annuus* begins to bloom. This is particularly noticeable at Topaz, Utah, where the host plant begins to bloom in late July. Here the earlier bloom is well attended by certain bees, such as *Dufourea marginata* (Cresson) and *Diadasia enavata* (Cresson). It is only when the above species decline in numbers that females of *triangulifera* become common. This apparent mistiming of *triangulifera* may be a mechanism serving to decrease competition at the pollen source.

Males are present throughout the nesting period, but they become scarce sooner than the females. They often cluster at night on sweetclover and other tall plants in the vicinity of the nesting site. At Topaz, they were sometimes found on the same stem with males of *melanderi* but always in discreet groups. Cockerell (1898) records them clustered on flowers of *Aster*. Since males cannot always be found on plants at night, it is probable that, like *N. melanderi*, a greater or lesser number of them, depending upon climatic conditions, spend the night underground. A group of about 20 males was observed in a small subterranean pocket at the edge of the Topaz site. Both sexes take part in a weaving flight pattern over the nesting site. The hum produced by this flight is noticeably lower than that of *melanderi,* although the insects average only slightly larger.

Nest building. Without exception, each female constructs and provisions her own nest. Nests vary in their proximity. In the more crowded areas, they may be only ¾ inch apart and, at this density, they are often clustered in groups about the size of a man's hand. In less crowded areas, they may be scattered from one to five or more feet apart.

At the Lawrence site, bare sand was preferred over grassy areas for nesting, but several heavy concentrations were located in areas having a sparse growth of *Tribulus terrestris.* At Topaz, the most concentrated areas of nesting were on bare ground (Fig. 2) or where there was a sparse cover of salt grass. At the latter site, in areas where moisture was higher and the salt grass more dense, *N. melanderi* nests usually replaced those of *N. triangulifera.* Since some of the largest concentrations of nests at Lawrence were in small areas where the sand was shallow, it appears that the density of nests may be affected to some degree by the character of the substrate. In Kansas, nests begun late in the season were often built in the lee of dead branches and other sheltering objects.

Digging at Lawrence started at various hours during the day. This contrasts with the initial nest digging of *melanderi* in Utah, which always takes place in the late afternoon. The female first grasps the substrate with her mandibles, at the same time scratching vigorously with her fore and mid legs. If unsuccessful in loosening the crust, she usually flies a short distance and repeats the procedure. If successful, she uses her legs to push away the material loosened by her mandibles. She turns round and round, constantly repeating the digging and scraping procedure. In the sandy area at Lawrence, the top quarter-inch of crust proved the most difficult challenge and, after this crust was penetrated, digging proceeded at a rapid rate. Several one-day-old nests excavated in this area consisted of straight vertical shafts 36-66 cm. deep and had variously shaped dilations along their walls.

A picture of the nest-building sequence was obtained at the Lawrence and Topaz sites from the excavation of about 35 nests. First, the main tunnel is excavated (probably within the first 24 hours). This tunnel may be vertical or else inclined at various angles for a few centimeters before descending vertically (Fig. 4). In the sandy site at Lawrence its depth ranged from 50 to 110 cm., with an average of about 70 cm. Similar nest depths were observed in the sand dunes at Cornish. Five nests dug in the silt loam of the Topaz site averaged about 37 cm. and a number of nests in the heavier, wetter soil at Amalga, Utah, averaged 48 cm. The latter figure corresponds well to those of both Pierce and Rau (1904, 1929) who found nests descending to about 50 cm. in soil they described as a heavy clay. The diameter of the main shaft is nine mm. At the surface where it joins the vestibule the burrow narrows to about 7.5 mm. This narrowing of the main burrow at the entrance is common to the halictid bees and distinguishes their nests from those of andrenids and melittids.

At the Topaz site, the main shafts were more or less smooth and even in diameter, although they often had several short lateral branches; at the sandier Lawrence site they usually had numerous irregular dilations and lateral cell- and tunnel-like excavations. These dilations and excavations appeared to be made to obtain the fine silt particles with which the cells, cell laterals, and at least portions of the main shaft were lined.

In contrast to this situation the nests constructed in the sand dunes at Cornish, where there were no silt strata, had neither burrow dilations nor silt-lined cells and tunnels. Since the burrow walls at Cornish appeared to be lined with slightly finer sand grains than average for the surrounding soil, it appears that the species always lines its burrows with the finest materials available in the soil contacted during nest excavation.

The early tumulus is large (commonly about nine cm. in diameter), circular, and somewhat flattened on top. In this stage the nest entrance is located centrally in the tumulus and is often exposed (Fig. 4A). As excavation of the nest progresses, the tumulus comes to resemble a cone of loose soil which covers the entrance hole (Fig. 4B). After the first two or three days, the female begins to force her way laterally through the loose tumulus rather than from above, eventually forming a horizontal vestibule. The vestibule may be 5-10 cm. in length and is dug into the substrate as well as being formed from the tumulus (Fig. 4C). As wind erosion proceeds, the original tumulus becomes a scarcely visible elongate hump, having the nest entrance at its perimeter; finally only the tubular chimney remains (Fig. 5). The persistence of the vestibule even in such pure sand areas as Cornish indicates that it is lined with some form of cement.

When the bee leaves the nest, she pauses to kick the vestibule full of loose sand. Upon returning she tunnels her way without pause through this plug, with the result that the vestibule is often partially destroyed. On one occasion, a bee was seen to carry damp sand from within the burrow and plug the entrance with it, but this may not be the usual procedure. At the Lawrence site, damaged vestibules were not repaired after nest construction was well under way. No fresh sand was noted outside the nest entrance after the vestibule had been constructed and plugged, and it is assumed that the sand resulting from further excavation was distributed into the various dilations and excavations of the main shaft. At the Cornish site, where no dilations are formed, the sand from late digging is apparently deposited in a vertical extension of the main burrow.

At the Lawrence site, the cells are vertically arranged and evenly spaced along one and sometimes two cell laterals (Fig. 6A-B). They are usually from two to three cm. apart as measured from the center of one cell opening to the center of the next. The cell laterals have the same diameter as the main shaft and vary in length, depending upon the number of cells pendant from them. The longest primary lateral seen had 12 cells and was 33 cm. long; the shortest had seven cells and was 20 cm. long. The primary lateral is usually curved gently in the horizontal plane, so that all cells along it are at about the same depth (Fig. 6A-3). In one case, the primary lateral was forked 4 cm. from the main shaft. One branch was 4.5 cm. long and carried only one cell, which was the seventh to be constructed in a series of eight. The primary lateral is provided with from 6 to 13 cells before it is completed and a new lateral begun. This second lateral may be above, on the same level with, or below the first, but the last situation seems to be the most common. The second lateral is short (the longest, six cm.) and carries at most two cells (Fig. 6B). At the Topaz and Cache Valley sites there are often several cell laterals, each of which is short and carries only a few cells.

At Lawrence the basal cell along the primary lateral is usually from 3.5 to 10 cm. from the main shaft. There is evidence, however, that the first cell to be excavated and completed is constructed from 7 to 10 cm. from the main shaft, and that later cells may be added between this cell and the main shaft. In a general way, a sequence of cell building along the cell lateral is followed in which consecutive cells are placed next to each other, the oldest closest to and the youngest farthest from the main shaft. That these sequences are not exact is apparent from two examples. Using the smallest numbers for the oldest cells, one 10-cell series was described in our notes as follows: shaft-10-6-1-2-3-4-5-7-8-9, and another series with eight cells: shaft-7-8-1-2-6-3-4-5.

Cells are first excavated as rough cavities in the sand and then given their final shaping with a lining of clay or, at least, fine particles of soil. The finished cells are narrow and taper more gradually toward the neck than those of most other halictine bees. The cell of *N. melanderi* is considerably more oval. Cell length from floor to ceiling is 20-22 mm., with a maximum width of 8.5 mm. When sealed the two ends of the cell have about the same taper and the side walls are nearly parallel (Fig. 7). The ceiling tapers more than that of *N. melanderi* and the spiral structure is less obvious. Although the building sequence is not readily determined from the finished structure, the ceiling is constructed like a coiled rope and the plug is added later. Above the ceiling, the neck, which is packed with sand, is about 6 mm. wide and 8-10 mm. long. The cell linings are smoothed and polished, but not to the extreme brightness found in the cells of *melanderi* and many other solitary bees. The lower 13 mm. is provided with a thin, waxy coat that becomes gradually thicker toward the bottom of the cell (Fig. 8).

The rate of cell construction and cell provisioning is not known, but two nests known to be 16 days old contained 8 and 10 completed cells. The maximum number of cells found in a completed nest was 15, with an average of 10 or 11.

After receiving its full complement of cells, a lateral is completely plugged with sand excavated from the main shaft (Fig. 6).

Provisioning. It is apparent that *triangulifera* prefers *Helianthus annuus* as a pollen source. However, there is evidence that it is not monolectic. A few females, some with pollen loads, have been taken on *Bidens involucrata, Grindelia squarrosa, Helianthus lenticularis, Rudbeckia triloba,* and *Silphium perfoliatum,* as well as *H. annuus.* Males have been taken on a variety of plants, including *Cleome serrulata, Medicago sativa, Bidens involucrata, Gilia* sp., *Grindelia squarrosa, Helianthus lenticularis, H. petiolaris, H. maximiliani, Polygonum* sp., *Rudbeckia triloba, Silphium perfoliatum, Solidago* sp., *Vernonia* sp., and *Aster* sp.

The number of foraging trips required to provision a cell is not known. However, at the Lawrence site, females presumably actively collecting spent from 1.5 to 2.5 hours per trip and remained in the nest from 9 to 15 minutes between trips. At this site probably little or no time was spent in travel to and from the pollen source since the immediate area abounded in *Helianthus*. *N. triangulifera* usually carries an enormous pollen load, and probably no more than four trips are needed to supply a cell. Pollen is carried on the hind legs and also on the sides of the propodeum and the venter and sides of the abdomen (Fig. 9) where bands of scopal hairs are present on segments 2-6 (Fig. 10).

The female behaves in a distinctive manner while collecting pollen. She crawls over the disc-flowers with a wading motion, waggling her abdomen vigorously from side to side. Her fore and midlegs clean pollen from the head and thorax and pass it to the scopa of the hind legs. The pollen she collects on her abdominal venter is repeatedly packed down with her hind legs.

The pollen is deposited in the cell without the addition of any nectar. Presumably, the latter is added at the time the entire food mass is shaped.

The pollen mass is distinctively shaped (Bohart, 1952). It is gently rounded on its upper surface, its edge forming a narrow flange by which it is suspended from the tapering wall of the cell (Fig. 4G). On close examination it can be seen that the top of the mass is formed as a lid fitting into the flanged, bowl-shaped lower portion. Beneath this flange, the mass conforms to the shape of the cell bottom, but it is usually separated from the floor by a narrow space. Dimensions of the pollen mass are approximately 8.2 by 4.5 mm. The provisions are as moist as they can be without losing shape, and they remain so until consumed (Fig. 11).

After the nest is completely provisioned, the female fills the lower portion of it with sand obtained from the walls of the main shaft and its various enlargements. As a result, the upper open portion contains many horizontal and oblique cell-like burrowings (Fig. 6).

Like many other halictines, the female of *N. triangulifera* shows little hesitation in entering her nest after returning from a flight. Recognition is probably by landmarks. When the nest was caged by the observer, when it had been stepped on, or when unfamiliar objects were placed close by, the returning bee made brief erratic attempts to find it, after which she left the area for varying periods of time, sometimes for an hour or more. This procedure was repeated until the nest opening was uncovered or until she found it herself. When the nest was undisturbed, entry was swift, the bee alighting suddenly (sometimes appearing almost to "dive") at the nest entrance and working her way quickly through the sand plug.

Females apparently spend the night in the nest after the main burrow is constructed. When the nest is complete and its lower portions are plugged as described above, the female remains in the nest, apparently leaving it only to feed. After the nesting season it was common to find the females dead at the bottom of the open portion of the nest (Fig. 6).

Development. The egg is laid on top of the completed pollen ball just before the cell is sealed. It is cylindrical and very gently curved, measuring 3.7 by 0.9 mm. It is affixed to the pollen cake at both ends and, since the mass is slightly flattened at the summit, there is usually a little space under the middle (Fig. 11). The egg of *melanderi* is considerably longer and more arched. Eggs in the laboratory at 72° F. hatched in a maximum of 2½ days. The total incubation period is probably a few hours longer than this.

The head capsule widths of 40 larvae of various sizes from the Lawrence site were measured. No clear indication of the total number of larval instars was obtained from this small sample, since capsule width in the smaller larvae varied considerably. However, the last two instars could be clearly distinguished. The average capsule width of the penultimate instar was 1.28 mm. ± S. E. .01, and that of the ultimate instar 1.61 mm. ± S. E. .02. The capsule width of the prepupa was identical to that of the ultimate larval instar, as would be expected, since there is no molt involved in the transformation. Unpublished measurements by Bohart of a larger series of *N. melanderi* larvae in Utah suggest the presence of four larval instars, although the possibility of some early molts without appreciable change in size has not been ruled out. The honey bee is reported to have five larval instars (Bertholf, 1925).

The length of the larval feeding period is not known with certainty. The 16-day old nests previously referred to contained at least one fully fed larva beginning to defecate. If one can judge from *melanderi,* the first egg is laid on the day after the nest is started or on the following morning. If the egg stage lasts 2½ days, the larvae must feed for a period of between 10 and 12 days.

During its early instars the larva feeds while lying ventral-side down on top of the pollen mass. The head is swung back and forth as the pollen grains are scraped out of the mass, leaving a shallow, oval basin (Fig. 12). What appears to be the third instar shifts in position when the basin reaches the edge of the ball, thus making the basin more transverse. With several more shifts the basin extends around the ball until the larva is perched on an "island" in the center. During this period the flattened venter and lobate expansions of the ventro-lateral margins of each segment are quite in contrast to the more cylindrical shape and smoother outline of *N. melanderi* larvae. This applies particularly to instars after the first (Fig. 13). After the final molt the larva starts to feed on the edge of the ball and soon thereafter it curls vertically around the ball but maintains its position on top. The major portion of the food supply is consumed during this stage. The final fragment to be eaten is cradled between the ventro-lateral lobes of the penultimate abdominal segment. *N. melanderi* feeds in a similar manner, but the third instar reaches farther down on the ball and does not circle it completely, thus leaving an asymmetrical mass for the next instar.

The larvae in early stages refused to feed in the laboratory at temperatures of 80° F. and above, in contrast to larvae of *melanderi*, which developed best at about 84° F. *N. triangulifera* larvae were seen to feed between 70° and 75° F., but careful rearing studies were not attempted. This difference between feeding temperature tolerances is probably associated with the greater depth and consequent cooler temperature of *triangulifera* brood cells.

The slightest drying of the food mass causes an early instar larva to stop feeding. When refusing to feed, it elevates the anterior third of its body into a nearly vertical position, thus giving it a pronounced sway-backed appearance. The final instar is not quite so sensitive to changes in condition of the food, but when it tries to feed on a mass that is too dry, the pollen scraped off by the mandibles forms little balls that are discarded (Fig. 14).

When the pollen mass remains in the proper moist but solid condition, it is always completely consumed. If the final instar is unable to finish a desiccated or moldy food supply, development usually proceeds to a dwarfed prepupa. When very dwarfed, the prepupa is C-shaped instead of 7-shaped (Fig. 15) and probably cannot pupate successfully.

Defecation commences a day or two after feeding is completed. The feces are bacilliform when extruded, but are flattened by the posterior end of the larva into short strips after being deposited in the bottom of the cell. The brownish-orange strips are arranged radially around the cell bottom and do not extend far up the walls as they do in *melanderi* cells (Fig. 7). After the last fecal pellet is extruded, a dark brown, sticky, excretory material is produced.

In some cases it remains as a transverse bar on the venter of the body and in other cases it is smeared onto the fecal strips.

Transformation to the rigid prepupa (Fig. 13) takes place immediately after defecation is completed. The variation in prepupal color previously referred to appears to be associated with cell temperature. In Utah the month of September, 1959, was cool and damp. Most of the prepupae formed in late August and early September were pale, and many were white. Examination of the fecal strips revealed nothing but sunflower pollen shells. Apparently, the yellow prepupal color is derived from an oil in the sunflower pollen which only colors the integument at warm temperatures.

Nomia nevadensis arizonensis Ckll.

This small bee is found from central Utah to central Jalisco, Mexico, and from western Arizona to western Texas. Fragmentary observations were made at a nesting site about three miles north of Delta, Utah. The site is situated on a north-sloping bank about 15 feet above the Sevier River. The area is evenly vegetated with salt grass (*Distichlis stricta*) interspersed among scattered greasewood plants (*Sarcobatus vermiculatus*). The soil is a silt loam underlain by alluvial gravel at a depth of about 42 cm.

Observations were made on August 17, 1955, at which time nesting had just begun. The nests were scattered throughout the site in rather loose aggregations. Four were excavated and, although none were complete, it could be seen that their plan was similar to that of *N. triangulifera* (Fig. 4E). The entrance was at one side of the tumulus and the burrow was a straight vertical shaft or was slightly inclined for a few centimeters before it turned vertically. The diameter of the shaft was 7.7 mm. The total depths of the nests examined ranged from 23 to 42 cm. Seven cells were examined. Two were being provisioned, three were complete with pollen and egg, and two contained larvae. The cells were similar to those of *N. triangulifera*, but slightly more oval. They measured approximately 19 by 7 mm., tapering to 4 mm. at the neck. As in the case of *N. triangulifera* cells, they were suspended vertically from a horizontal lateral burrow which was sometimes slightly curved (Fig. 4E-7). In one nest, the first cell along the cell lateral was about 20 mm. from the main shaft, a second was 15 mm. beyond this, and a third was 15 mm. farther on. The lateral was excavated for 10 mm. beyond the last cell.

The pollen mass resembled that of *N. triangulifera* but was deeper, more angular beneath the flange, and had several characteristic seams along the bottom (Figs. 4F and 16). The egg was similar in size to that of *triangulifera*, but was somewhat longer and more arched like that of *N. melanderi* (Fig. 16). The growing larvae were likewise somewhat intermediate, but were shaped more like those of *triangulifera*. The dorsolateral prominences of the prepupa were less pronounced than those of *triangulifera*, but they were equally sharp (Fig. 3). Nearly all of the prepupae were light yellow, but a few were nearly white. Pollen shells taken from fecal strips in a cell with a white larva were from saltcedar (*Tamarix gallica*). Those from several cells with yellow larvae were of gumweed *(Grindelia squarrosa)*. The differences in larval color observed probably resulted directly from coloring materials in the pollens consumed.

Two young females were found in the main shaft of one nest. One carried some pollen on its hind legs. This suggests the possibility that more than one female may occupy a nest; however, it is believed that the presence of the second female was accidental, since we have repeatedly observed that females without a nest of their own may often "inspect" burrows being constructed by their neighbors.

No freshly dug earth was seen on the site during the early forenoon, but it was evident around many nests at 5:30 p. m., indicating that digging takes place in the late afternoon.

Females were collected frequently on gumweed flowers and occasionally on saltcedar, but none were taken on sunflower, even though it was common in the vicinity of the site. This species was reported as an effective pollinator of alfalfa in the Imperial Valley of California, (Linsley, 1946), but it has never been found on alfalfa in Utah, even when the nesting site is adjacent to an alfalfa field.

At 80° F. and 75 percent relative humidity *nevadensis* remained in the pupal period an average of 11 days as compared with 14 days for *triangulifera* and 12½ days for *melanderi*. In this group of species, length of the pupal period appears to be associated with size rather than phyletic proximity.

Nomia (Dieunomia) heteropoda Say[5]

This species is found from Maryland to western Arizona and southwest Utah, and from Minnesota to Texas. It was found nesting with *N. triangulifera* in the alluvial sand deposits at Lawrence.

The nests were rather uncommon and usually widely scattered, although some loose aggregations of four or five were seen. Little is known of the nesting habits of this bee. Blair (1935) reports that Mickel and Dawson found them nesting in sand, and that the burrows "extended down into the sand vertically for a distance of three or four feet."

On September 11, 1954, one nest of this species was excavated by Cross and Rettenmeyer (Fig. 6C). The tumulus and horizontal chimney were as described for *Nomia triangulifera.* The main shaft extended vertically to a depth of 94 cm. The top 80 cm. of this shaft were in sand, the remaining 14 being in the underlying silt bed of the original ox-bow lake. The walls of the tunnel in the sandy portion were completely straight except for one dilation at a depth of 30 cm. This portion of the shaft was lined with clay as described for *N. triangulifera.* The 14 cm. in the silt layer included an irregular mass of tunnels and cell-like excavations arising from the main shaft. Many of these were packed with sand, others were open. It seemed obvious that the clay from these excavations was used to line the main shaft, cell laterals, and the cells.

One cell lateral was present at a depth of 50 cm. This lateral was 16 cm. long, and it, as well as the main shaft, had a diameter of 13 mm. Two cells were present on the lateral, and were vertical with their entrances along the bottom of the cell lateral as described for *N. triangulifera.* The more basal cell was about 8 cm. from the main shaft, and the second was 6 cm. beyond the first (measured from the center of the plug of one to the center of the plug of the other). The clay-lined cells were very large, measuring 56 by 11.5 mm., and were long and narrow, with little taper. The more distal of the cells was the younger and had not yet been provisioned, although it was complete. The more basal cell contained a pollen mass and egg. The shape of the pollen mass and the position of the egg were as described for *N. triangulifera.* Dimensions of the pollen mass were 11.5 by 6.4 mm. (Fig. 6H).

The females visited the flowers of *Helianthus annuus* in company with *N. triangulifera.*

TABLE 1.—Comparisons of three subgenera of *Nomia.*

	Epinomia (*N. triangulifera* & *N. n. nevadensis*)	*Dieunomia* (*N. heteropoda*)	*Acunomia* (*N. melanderi*)
Nest entrance plugged	yes	yes	no
Horizontal "vestibule"	present	present	absent
Nest depth	21–110 cm.	about 100 cm.	usually about 22.5 cm., rarely to 35 cm.
Cell arrangement	evenly spaced along horizontal laterals	evenly spaced along horizontal laterals	in loose clusters
Cell shape	relatively long and thin. Taper slowly and evenly to neck.*	relatively long and thin. Taper slowly and evenly to neck.	relatively "jug-shaped." Taper rather sharply to neck.
Cell lining	dull to moderately bright	dull to moderately bright	mirror-bright
Interior face of cell plug	not obviously spiralled	not obviously spiralled	obviously spiralled
Shape of pollen mass	see description and figures	see description and figures	a dorsoventrally compressed ball
Fecal deposit	nearly confined to cell floor	....	extending ⅓ cell height
Pollen sources	usually Compositae	Compositae	Leguminosae and others, but rarely Compositae
Flight period	August and September	August and September	late June to late August
Optimum temperature for growing larvae	70° F. (for *triangulifera*)	....	85° F.

* Cells of *nevadensis* slightly more oval than those of *triangulifera.*

TABLE 2.—Mechanical composition of Utah soils used for nesting by *Nomia triangulifera* Vach.

Location	Depth in inches	Mechanical composition, percent				Texture description
		Sand*	Silt**	Fine† clay	Coarse‡ and fine clay	
Pleasant Valley	0–4 4–8	18 9	54 60	28 31	45 47	clay loam clay loam
Myton	0–4 4–8	46 45	36 38	18 17	21 19	sandy loam sandy loam
Topaz	0–4 4–8	45 16	39 64	16 20	24 31	loam silt loam
Hinkley	0–4 4–8	15 17	61 60	24 23	32 30	silt loam silt loam
Trenton	0–4 4–8	16 12	67 69	17 19	33 36	silt loam silt loam
Amalga	0–4 4–8	18 13	68 71	14 16	26 29	silt loam silt loam
Benson Ward	0–4 4–8	42 36	46 47	12 17	22 26	loam loam
Cornish	0–4 4–8	93 93	4 5	3 2	4 4	sand sand

* Particle diameters between 2.0 and .05 mm.

** Particle diameters between .05 and .002 mm.

† Particle diameters less than .002 mm.

‡ Particle diameters less than .005 mm. This includes silt particles between .005 and .002 mm.

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FIG. 1. Male *Nomia triangulifera* at entrance of nest containing female. Topaz, Utah, August, 1955.

FIG. 2. Nesting site of *N. triangulifera*. Variously shaped tumuli indicate nests in different stages of development. Topaz, Utah, August, 1955.

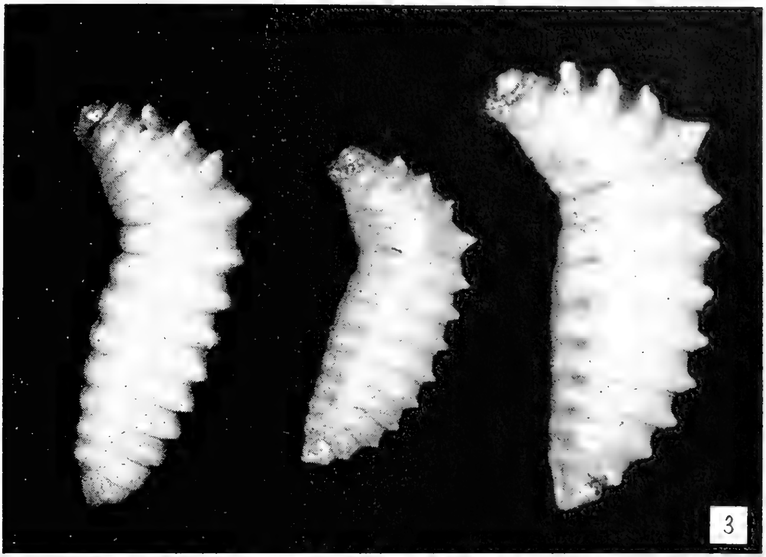

FIG. 3. Prepupae of (left to right) *Nomia melanderi, nevadensis,* and *triangulifera.*

FIG. 5. Wind-blown tumulus of *Nomia triangulifera* seen from above. Note horizontal plugged chimney and castings marking original extent of tumulus. Topaz, Utah, August, 1955.

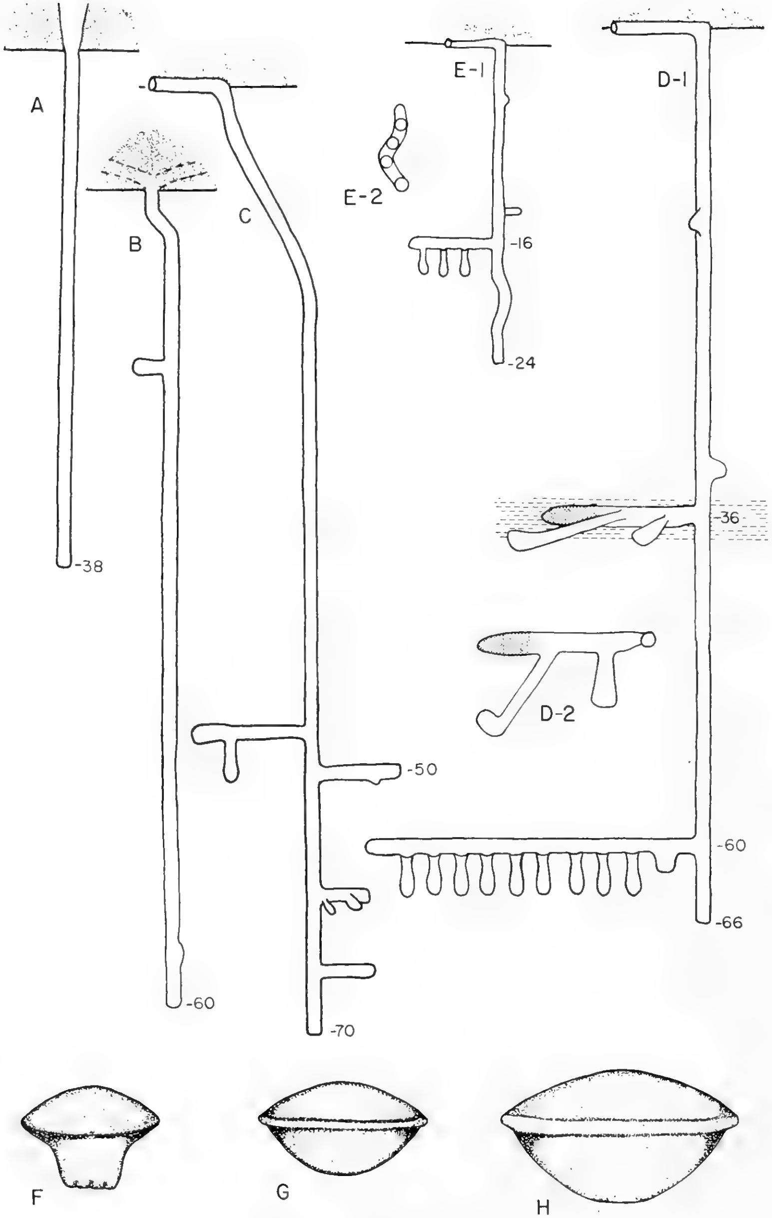

Fig. 4. A-D Vertical sections of *Nomia triangulifera* nests, Lawrence, Kansas, August, 1954. Numbers indicate depth in centimeters.

A. New nest showing truncate early tumulus and vertical entrance.

B. Nest 26 hours old showing transition to cone-shaped tumulus and loss of open, vertical entrance.

C. Slightly older nest showing lateral entrance and dilations and lateral branches of main tunnel.

D-1. Nearly completed nest. Lateral excavations in clay stratum. Apex of excavation packed with sand taken from cells.

D-2. Lateral at 36 cm. as seen from above.

E-1. Vertical section of *Nomia nevadensis arizonensis* nest. Delta, Utah, August, 1955.

E-2. Lateral at 16 cm. seen from above.

F. Pollen mass of *Nomia nevadensis arizonensis.*

G. Pollen mass of *Nomia triangulifera.*

H. Pollen mass of *Nomia heteropoda.*

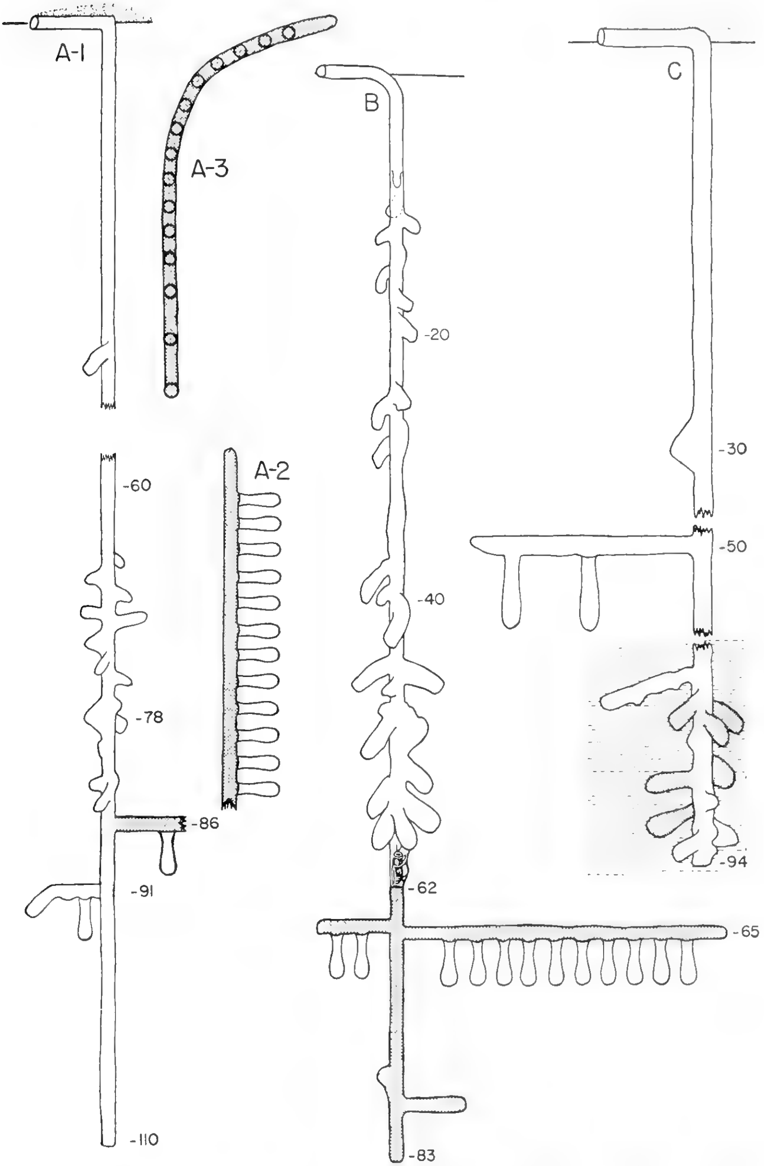

FIG. 6. A-B Vertical sections of *N. triangulifera* nests, Lawrence, Kansas, August, 1954. See Figure 4 for explanation of numbers.

A-1 and A-2. Nearly completed nest with primary cell lateral completed and packed with sand. Secondary lateral with one cell.
A-3. Primary cell lateral as seen from above.
B. Completed nest. Dead bee in tunnel at 62 cm. (tumulus as in Figure 5).
C. Nest of *Nomia heteropoda*, Lawrence, Kansas, September, 1954.

FIG. 7. Vertical section of sealed *Nomia triangulifera* cell with prepupal bee above fecal deposit. (Cell lined with mold hyphae.)

FIG. 8. Vertical section of *Nomia triangulifera* cell ready for provisioning.

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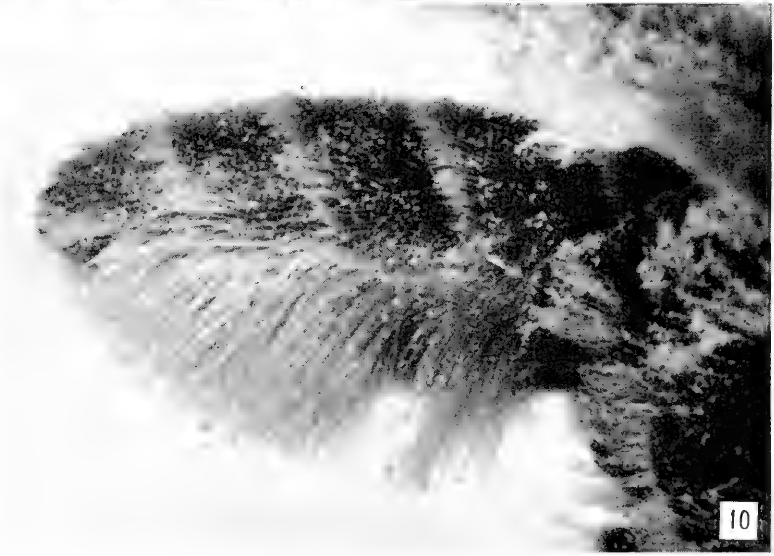

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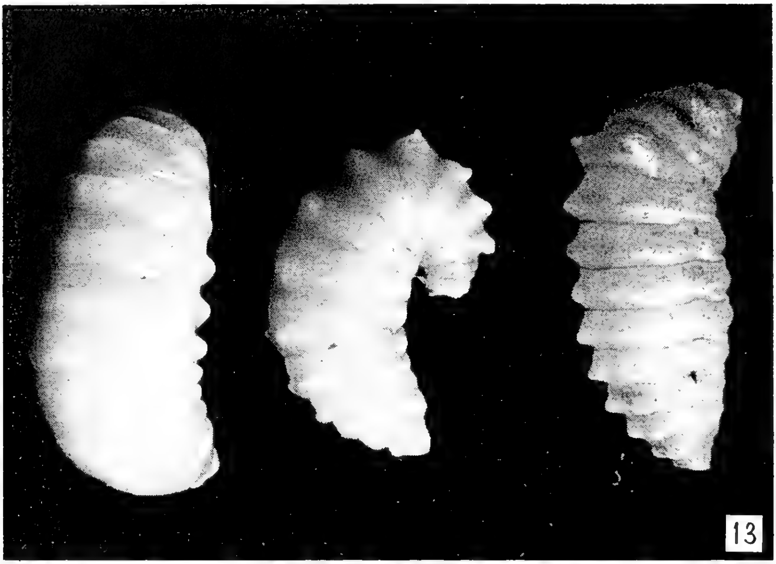
FIG. 9. Female *Nomia triangulifera* entering nest with load of pollen.

FIG. 10. Abdomen of *Nomia triangulifera* showing sternal scopa. (Photo by C. W. Rettenmeyer.)

FIG. 11. Pollen mass and egg of *Nomia triangulifera* (note moist condition of pollen).

FIG. 12. Pollen mass and fully fed first instar larva of *Nomia triangulifera*.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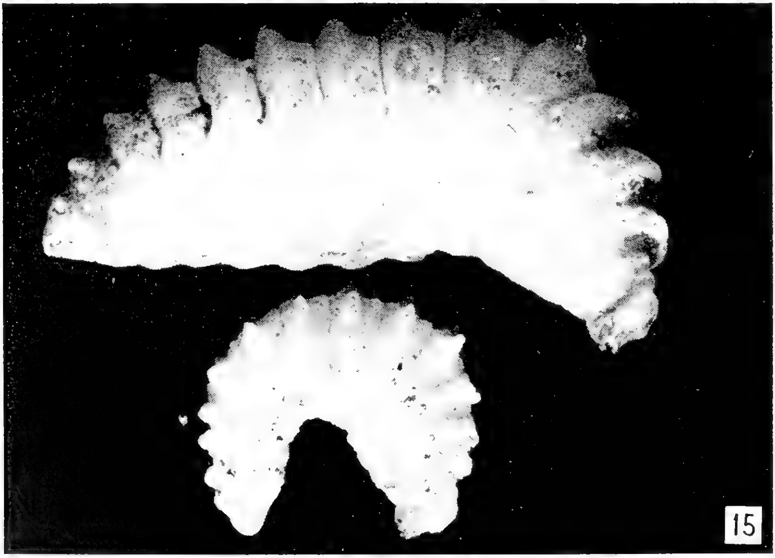
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FIG. 13. Final instar larva (left) and transition to prepupa (right) of *Nomia triangulifera*.

FIG. 15. Normal (left) and dwarfed (right) prepupae of *Nomia triangulifera*.

FIG. 14. Final instar larva of *Nomia triangulifera* feeding on an excessively dry food mass.

FIG. 16. Cell of *Nomia nevadensis arizonensis* with pollen mass and egg.

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A Revision of the Genus *Iva* L.

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ABSTRACT: This revision treats *Iva* in a broad sense, placing in synonymy several genera previously considered distinct by some early authors. In addition, the monotypic genus *Oxytenia* Nutt. is included in *Iva*. The fifteen species recognized include one proposed new species and several new combinations. The species are divided into three sections, based on comparative morphology and available cytological information. A phylogenetic interpretation of the genus is presented, and probable relationships with other genera are discussed.

INTRODUCTION

The North American genus *Iva* has been a source of difficulty both nomenclaturally and morphologically for a number of years. While various segregate genera have been proposed at one time or another, the present treatment considers the genus in a broader scope, recognizing that the several segregate groups are not at all sharply differentiated from one another, but rather they represent gradual transitions in the genus as a whole.

Most of the species are quite distinct from one another, and natural interspecific hybrids have not been found. However, intervarietal hybridization apparently occurs in *Iva annua* where the ranges of variety *caudata* and *annua* overlap. Several attempts to produce intra- and intersectional hybrids among the various species were unsuccessful. Artificial interspecific crosses usually resulted in no seed set or selfing.

While this treatment has been confined mainly to a morphological approach, an attempt has been made to incorporate the cytological data that have been obtained. Chromosome counts have been compiled for 11 of the 15 species included in the genus, and this information has been a valuable supplement to morphological study in indicating probable relationships in the three main evolutionary lines.

TAXONOMIC HISTORY

Iva was founded in 1753 by Linnaeus in the *Species Plantarum.* At that time *I. annua* and *I. frutescens* were the only species included in the genus. *Iva annua* was first described by Linnaeus in *Hortus Uppsalicus* and is the type of the genus. However, the epithet *I. ciliata* Willd. has been consistently misapplied to *I. annua* L. by both European and American botanists.

As recognized here, *Iva* consists of 15 species with several subspecies and varieties. With the exception of *I. acerosa (Oxytenia acerosa* Nutt.), most of the species were previously placed in *Iva* by Gray (1886), and his treatment is generally followed by other conservative workers in the Compositae. However, some authors have proposed various segregate genera based mainly on inflorescence and paleae characteristics.

Gray (1886) and Hoffman (1894) employed three sections in *Iva.* These were *Cyclachaena, Chorisiva,* and *Euiva.* The two former sections were recognized as distinct genera by Rydberg (1922) while Fresenius (1836) and Torrey and Gray (1841) treated *Cyclachaena* as a separate genus. However, Gray (1886) later used the name *Cyclachaena* to denote a section of *Iva* and thereafter considered it a natural section of this taxon. The genus *Euphrosyne* has been confused with *Iva* in the past, and *Iva ambrosiaefolia* was originally described by Gray as a species of *Euphrosyne.*

Rydberg (1922) used *Iva* as the type genus of his tribe *Iveae,* one of two tribes he recognized in the Ambrosiaceae. The tribe *Iveae* contained seven genera, *Iva, Leuciva, Oxytenia, Chorisiva, Euphrosyne,* and *Dicoria.* Of these, all but *Euphrosyne* and *Dicoria* are considered herein to belong to *Iva.*

CYTOLOGICAL OBSERVATIONS

METHODS

Immature heads for cytological study were fixed in a mixture of one part of propionic acid and three parts of absolute ethyl alcohol. Fixation was for a period of at least 48 hours to several weeks. Material kept longer than a week was transferred to 70 percent alcohol and stored in the refrigerator until used.

For study of microsporocytes, entire disc corollas were cut away from the ovary and macerated in iron-proprionocarmine stain with a fire-polished glass rod. After staining and heating, usable slides were made permanent by introducing a Venetian turpentine and propionic acid mixture under one side of the cover glass while withdrawing the stain from the opposite side with filter paper.

Diakinesis, telephase I, and prophase II stages were found suitable for determining chromosome number. Approximately 10 good cells were counted in each species reported. However, the count for *Iva imbricata* was made from a single mitotic prophase cell of anther tissue inasmuch as usable meiotic stages of this species were not found in the material studied.

Observations

Heiser and Whitaker (1948) reported the first chromosome number for *Iva*. They listed *I. axillaris* as having $n = 16$ to 17, but Peter Raven (Univ. of Calif. L. A., unpubl.) has recently found $n = 18$ in a plant of this species. During this study, the count of *I. annua* by Heiser and Smith (1955) has been verified, and chromosome numbers of nine additional species have been determined. These, together with pertinent collection data, are listed in Table 1. All counts are represented by voucher specimens deposited in the University of Kansas Herbarium. Camera lucida drawings of cells upon which most of the counts were based may be seen in figures 1 to 10. Attempts to obtain cytological material of *Iva nevadensis, I. hayesiana*, and *I. cheiranthifolia* thus far have been unsuccessful.

In checking the chromosome numbers listed in Table 1, it can be seen that haploid numbers of 16, 17, and 18 are each representative of several species. *Iva dealbata* with $n = 36$ is considered a tetraploid. One observation of *I. axillaris*, not listed in Table 1, was from a population of triploid plants from San Juan County, New Mexico. At diakinesis and metaphase I, many trivalents could be observed, but a count could not be made accurately.

PHYLOGENETIC CONSIDERATIONS

In *North American Flora*, Rydberg (1922) treated *Iva* as a genus of the tribe Iveae, one of two tribes he recognized in the family Ambrosiaceae. This treatment more or less followed some earlier workers, notably Britton and Brown (1913), in splitting the Compositae into three families. In this paper, *Iva* is considered to be a genus of the family Compositae and to belong to the subtribe Ambrosiinae of the tribe Heliantheae. This essentially follows Bentham's (1873) treatment in which he states that the Compositae represent "the most distinct, and the most uniform, and therefore the most natural, of all orders of phanergamous plants."

TABLE 1.—Chromosome numbers and collection data for various species of *Iva*.

Species	Chromosome number	Collection data
I. angustifolia	n=16	8 miles southeast of Wagoner, Wagoner Co., Oklahoma. *Jackson 2222*
I. texensis	n=16	railroad embankment, 8.1 miles south of Falfurrias, Brooks Co., Texas. *Jackson 2505*
I. asperifolia	n=16	sand dune facing the Gulf of Mexico at Tecolutla, Veracruz, Mexico. *Jackson 2543*
I. microcephala	n=16	grown from seed: East of Geneva and St. John Rd. Sandy alluvium of pasture. Seminole Co., Florida. *R. Kral 5235*
I. annua	n=17	city limits, Lawrence, Douglas Co., Kansas. *Jackson 2734*
I. imbricata	2n=ca. 34	sandy beach at Naples, Florida. *A. M. Torres*
I. frutescens ssp. *frutescens*	n=17	salt marsh, Galveston Island, Galveston, Texas. *Jackson 2533*
I. acerosa	n=18	Bernalillo, Sandoval Co., New Mexico. *Jackson 2506*
I. xanthifolia	n=18	Bernalillo Co., New Mexico, Tree Springs in the Sandia Mts. *Jackson 2732*
I. ambrosiaefolia ssp. *ambrosiaefolia*	n=18	grassland wash, 40 miles south of Villa Ahumada, Chihuahua, Mexico. *Jackson 2729*
I. dealbata	n=36	40 miles north of Entronque, Durango, Mexico. *Jackson 2728*

Generally considered to be closely related to *Iva*, as recognized here, are *Euphrosyne* (Ambrosiinae) and *Parthenice* (Melampodinae). However, both genera are easily distinguished from *Iva* by their strongly flattened achenes. In addition, the achene of *Parthenium* is shed with the paleae of the two opposing disic flowers attached to it, and *Euphrosyne* has distinct corky margins on the achene. Neither of these characters occur in *Iva*. Cassini (1834), Bentham (1873), and Small (1917) have previously commented on the relationship of *Iva* to the subtribe Melampodinae of the tribe Heliantheae. According to Small (1917), "the affinity between *Iva* (Ambrosiinae) and *Parthenice* (Melampodinae) is so close that there can be no doubt of the systematic position of the Ambrosiinae in the Heliantheae and also very little doubt, if any, of the origin of the subtribe from the Melampodinae via *Parthenium, Parthenice, Cyclachaena* and *Iva.*" Wodehouse (1935) has supported this statement with evidence from studies of comparative pollen morphology in the Ambrosiinae. The position of the Ambrosiinae as a subtribe of the Heliantheae has been accepted in a relatively recent paper by Cronquist (1955). *Iva,* then, and the remainder of the Ambrosiinae are connected to the Heliantheae by transitional forms of the Melampodinae.

In the Heliantheae, basic chromosome numbers of n = 4 to n = 19 are known to occur in various genera (Darlington and Wylie, 1955). In the subtribe Melampodinae, to which the closest relatives of *Iva* belong, basic numbers of 8, 9, 10, 17, and 18 occur in several genera. The haploid number of some species of *Parthenium* are reported as n = 17 and 18 (Rollins, 1950). Considering the lower numbers in the Melampodinae, the higher members such as 17 and 18 may be presumed to represent polyploid types. Thus *Iva* with n = 16, 17, and 18 apparently is a genus in which specific differentiation has occurred at the polyploid level, presumably following the origin of the group.

Within *Iva,* the cytological and morphological data point to three main lines of divergence. For purpose of clarity these will be discussed as species groups, but a formal taxonomic treatment is presented later.

In the first species group, consisting of *Iva microcephala, I. texensis, I. angustifolia,* and *I. asperifolia,* n = 16 was the only haploid chromosome number found. These species, particularly the latter three, are very closely related morphologically. *Iva microcephala,* with free phyllaries, three pistillate and up to six staminate flowers per head, may be considered more primative than the other three species with united phyllaries, one (rarely two) pistillate and a reduced number of staminate flowers. This group of species has thus undergone a reduction in number of pistillate and usually staminate flowers, and the phyllaries have progressed from free to united. Coincident with the reduction in number of flowers per head and the union of phyllaries, has been a marked tendency for those species having these characteristics to drop the entire head with the enclosed achene. This condition may have come about because the mature achene is tightly enclosed in the involucral cup. The inflorescence bracts of all the species are linear. Two of the species, *I. microcephalia* and *I. angustifolia,* are strictly annual while *I. tex-*

ensis and *I. asperifolia* appear to be biennial to perennial. The two latter species occur on coastal beaches or adjacent saline soils while the other two species usually grow farther inland.

The second species group, composed of *Iva imbricata, I. frutescens, I. cheiranthifolia, I. hayesiana, I. axillaris,* and *I. annua,* was found to have a chromosome number of n = 17 in those species studied. Although *I. cheiranthifolia* and *I. hayesiana* have not been studied cytologically, they nevertheless belong here because of morphological criteria. Due to conflicting reports or a variable chromosome number, *I. axillaris* is in need of additional cytological study. The species of this group comprise a part of *Euiva* as recognized by Gray (1886), Hoffman (1894) and Fernald (1950). The species are generally characterized by heads in spicate, spicate-racemose, or paniculate arrangements in the axil of leaves or leaf-like bracts that are usually linear-lanceolate to lanceolate. *Iva annua* is the only annual of this group and probably represents a derived condition from the frutescent coastal stock. *Iva axillaris,* a species frequently found in saline soils of the southwest and western U. S., appears to have been derived from *hayesiana*-like stock by a fusion of the phyllaries, reduction in size, and the development of a rhizomatous growth habit. With the exception of *I. annua* and *I. axillaris,* the species are usually found along the coastal areas of the United States, Canada, the Bahamas, and Cuba. *Iva hayesiana* of southern California and Baja California, Mexico, has probably moved inland somewhat from its original coastal habitat. Since *I. axillaris* usually occurs in saline inland soils, this might be considered similar to the brackish marshes and strand habitats of some of the other species.

The third species group, consisting of *I. acerosa, I. nevadensis, I. ambrosiaefolia, I. xanthifolia,* and *I. dealbata,* has a chromosome number of n = 18 or n = 36 in the species studied. *Iva nevadensis* has not been studied cytologically. Gray (1886) considered the three latter species to be closely related and placed them in the section Cyclachaena. This species group is held together by the (1) variously lobed or dissected leaves (coarsely serrate to lobed in *xanthifolia*); (2) large paleae of this pistillate flowers (paleae lost in one species); (2) reduction in size or complete loss of the pistillate corolla; and (4) flowers usually borne in ebracteate panicles. These represent also some of the lines of differentiation within the group. In *I. ambrosiaefolia* and *I. acerosa* the pistillate corolla has been completely lost. The small fleshy disc may or may not represent a rudimentary structure since it is found inside the corolla at the base of the style of both *I. nevadensis* and *I. xanthifolia.* Plants of *I. xanthifolia* have a corolla on some flowers and on others it may or may not be found. Apparently this species represents a transitional form. In *I. dealbata* the paleae of both pistillate and staminate flowers have been lost and are found only rarely as a vestigial structure. All the species of this group are quite distinct from one another. Their distribution is mostly in the southwestern parts of the United States and adjacent Mexico, and none of the species inhabit coastal areas. *Iva xanthifolia,* a weedy species, has spread considerably outside the range of the other entities. Two of the five species are perennials.

On the basis of pollen morphology, Wodehouse (1935) chose *Parthenice* as the ancestral type of the Ambrosiinae and noted the following phylogenetic trends within the subtribe: (1) a reduction in size of spines and a thinning of exine; (2) a reduction in furrow length; and (3) increase in total size of the pollen grain. Furthermore, he derived *Iva nevadensis, I. ambrosiaefolia, I. xanthifolia,* and *I. dealbata* from *I. acerosa* by reduction of spines and a slight increase in size. It should be noted, however, that *I. dealbata* is a tetraploid, and that polyploid entities are known to have larger pollen grains than related diploid species in some genera. Nevertheless, the data from pollen studies and gross morphology are in rather close agreement. The fact that Wodehouse incorporated Rydberg's segregate genera in his phylogenetic scheme in no way detracts from its basic importance.

Insofar as pollen morphology is concerned, *I. acerosa, I. ambrosiaefolia, I. nevadensis, I. xanthifolia,* and *I. dealbata* of the third species group are characterized by having furrows that are elongate with the germ pores within. The remaining entities of the first two species groups have the furrows greatly reduced and generally represented by pits in the exine that scarcely extend beyond the enclosed germ pores.

Considering pollen structures, chromosome number, and gross morphology, the main lines of differentiation within *Iva* become apparent. Using these data, a phylogenetic interpretation of the genus is presented in figure 11.

ECONOMIC IMPORTANCE

The species of *Iva* have no known economic importance. A number of species do, however, cause hay fever and dermatitis (Wodehouse, 1945). *Iva acerosa* has been shown to cause dermatitis, and *I. xanthifolia* causes both dermatitis and hay fever. *Iva annua, I. frutescens,* and *I. axillaris* may cause hay fever where they are locally abundant. *Iva axillaris* and *I. xanthifolia* are able to absorb selenium compounds from the soil in sufficient quantities to make them poisonous to livestock. *Iva acerosa* is also said to be poisonous to animals.

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SYSTEMATIC TREATMENT

GENERIC DIAGNOSIS

Iva L. Sp. Pl. 988. 1753
Denira Adans. Fam. Pl. 2:118. 1763

Annual or perennial herbs or shrubs, glabrous or pubescent. Leaves up to 30 cm. long, alternate or opposite, entire, serrate, lobed, or pinnately divided. Inflorescence of heads in a spicate, spicate-racemose, or paniculate arrangement. Heads 2-8 mm. broad, containing both male and female flowers, the latter marginal. Involucre hemispheric or turbinate. Phyllaries 3-9, sometimes imbricate, free, or united. Staminate flowers 3-20, corolla funnelform, 5-lobed, glabrous or pubescent, up to 6 mm. long, stigma capitate-penicillate, penicillate, or peltate, one-half to almost as long as the stamens. Paleae of the staminate flowers filiform to spatulate, lacking in one species; those of the pistillate flowers linear to obicular, lacking in one species. Pistillate flowers 1-9, marginal, corolla truncate, up to 6 mm. long, rudimentary or absent, possibly represented by a fleshy disc at the base of the style in some species. Achenes 1-13 mm. long, cuneate to abovate, somewhat compressed, glabrous, resin-dotted, tubercled, or pubescent at maturity.

Type species: *Iva annua* L. Figures 12 to 16 represent botanical drawings of the type specimen.

As mentioned previously, data from studies of pollen structure, gross morphology, and cytology indicate three main lines of divergence in *Iva.* The following three sections are based essentially on these data.

DIAGNOSIS OF THE SECTIONS OF IVA

1. *Iva* section LINEARBRACTEA, sect. nov.

Bractis subtus capitulis linearis vel filiformis; phyllariis conjunctis vel si libris, illo cum 3 feminis floribus in singulis capitulis, phyllariis glandulosis punctatis, et foliis linearis; paleis filiformis vel linearis; achaeniis laevis vel cum paucis resinis punctis vel aliquando sparse pubescentis; foliis integeris serrulatis. Typus: I. microcephala Nutt.

Bracts subtending the heads linear or filiform; phyllaries united, or if free, then 3 pistillate flowers in each head, the phyllaries glandular-punctate, and the leaves linear; achenes glabrous and with a few resin dots or sometimes slightly pubescent; paleae filiform or linear; leaves entire or serrulate. Type: *I. microcephala* Nutt.

2. *Iva* Section IVA

Bracts subtending the heads not linear to filiform; phyllaries free, or if fused, then 5-8 pistillate flowers per head; paleae filiform to spatulate; achenes usually resin dotted; leaves entire to serrate. Type: *Iva annua* L.

3. *Iva* Section CYCLACHAENA (Fresen.) Gray emend.

Heads usually borne in ebracteate panicles or solitary in leafy branches; phyllaries free; paleae of the pistillate flowers usually broadly ovate to orbicular; those of the staminate flowers usually linear (paleae lost in one species); achenes smooth to villous; leaves serrate, lobed, or pinnately dissected. Type: *Iva xanthifolia* Nutt.

Key to the Sections and Species of Iva

1\. Leaves entire, serrulate to serrate, never lobed or dissected; pistillate corolla present; heads in spicate, spicate-racemose or leafy panicles usually borne in the axils of leaves or leaf-like bracts.

2\. Bracts subtending the heads linear to filiform; phyllaries united, or if free, then usually 3 pistillate flowers in each head, the phyllaries glandular-punctate, and the leaves linear. . . . . (Section Linearbractea)

3\. Phyllaries free, the backs glandular-punctate, usually three pistillate flowers in each head. 1. *I. microcephala*

3\. Phyllaries united, the backs not glandular-punctate, glabrous or slightly pubescent, usually 1 or rarely 2 pistillate flowers per head.

4\. Stems usually decumbent at the base and rooting at the nodes; leaves oblong; 3–9 staminate flowers per head. . . . . 2. *I. asperifolia*

4\. Stems usually erect and not rooting at the nodes; leaves linear to lanceolate; 1–5 staminate flowers per head.

5\. Annual with herbaceous stems; involucre 2–2.5 mm. long. 3. *I. angustifolia*

5\. Biennial or perennial with woody stems up to 2 cm. in diameter at the base; involucre 3–4.1 mm. long. . . . . 4. *I. texensis*

2\. Bracts subtending the heads not linear to filiform; phyllaries free, or if united, then 5–8 pistillate flowers in each head; leaves not linear. . . . . (Section Iva)

6\. Phyllaries free, plant not rhizomatous.

7\. Plants annual, stems herbaceous: phyllaries hispid; achenes with few to several resin dots; median leaves usually ovate.

8\. Achenes usually 2.5–4.5 mm. long.

9\. Bracts subtending the heads ovate to broadly lanceolate. . . 5. *I. annua* var. *annua*

9\. Bracts subtending the heads linear-lanceolate, candate-acuminate. 6. *I. annua* var. *caudata*

8\. Achenes usually 4.8–13 mm. long (known only as fragments from bluff dwellings). 7. *I. annua* var. *macrocarpa*

7\. Plants perennial, stems usually woody; phyllaries glabrous or puberulent; achenes covered with resin dots at maturity; median leaves lanceolate to obovate.

10\. Median leaves alternate, glabrous, and fleshy; phyllaries 6–9, imbricate. 8. *I. imbricata*

10\. Median leaves opposite, puberulent, not fleshy; phyllaries 4–6, not imbricated or only slightly so.

11\. Leaves serrulate to serrate.

12\. Leaves narrowly lanceolate to lanceolate, on flowering branches usually 5–8 times as long as broad, serrulate to serrate with usually 5–8 teeth per side. . . . . 9. *I. frutescens* ssp. *frutescens*

12\. Leaves elliptic to obovate, on flowering branches usually 2.5–4 times as long as broad, usually coarsely serrate with 8–17 teeth per side. 10. *I. frutescens* ssp. *oraria*

11\. Leaves entire.

13\. Heads in leafy panicles; phyllaries slightly membranaceous on the margins (known only from the West Indies). . 11. *I. cheiranthifolia*

13\. Heads in leafy racemes; phyllaries not membranaceous on the margins (known only from southern and Baja California). 12. *I. hayesiana*

6\. Phyllaries united, plants rhizomatous. . . . . 13. *I. axillaris*

1\. Leaves variously lobed or dissected; if only serrate, then the heads born in axillary or terminal ebracteate panicles; pistillate corolla lacking, rudimentary, or represented by a small fleshy disc. . . . . (Section Cyclachaena)

14\. Plants perennial; leaves pinnatifid with linear to filiform divisions or pinnately cleft and tomentose.

15\. Paleae present; leaves pinnately divided with linear to filiform divisions. . . . . 14. *I. acerosa*

15\. Paleae absent; leaves pinnately cleft, the divisions lanceolate or ovate, densley villous-tomentose. . 15. *I. dealbata*

14\. Plant annual, leaves pinnatified or lobed with rounded, obovate, or lanceolate divisions, not tomentose.

16\. Corolla of the pistillate and staminate flowers villous-pubescent; heads usually solitary and scattered in leafy branches. . . . . 16. *I. nevadensis*

16\. Corolla of the pistillate flowers absent, or if present, then vestigial and glabrous; staminate corolla glabrous; heads paniculate.

17\. Leaves serrate, sometimes 3– to 5–lobed, never pinnatifid. . . . . 17. *I. xanthifolia*

17\. Leaves pinnatifid.

18\. Pubescence of the stem appressed and hispid, not glandular in the upper branches. 18. *I. ambrosiaefolia* ssp. *ambrosiaefolia*

18\. Pubescence of the stem hispid below, hispid and glandular in the upper branches. 19. *I. ambrosiaefolia* ssp. *lobata*

1. *Iva microcephala* Nutt., Trans. Am. Phil. Soc. II. 7:346. 1840.

Annual; stem 4-10 dm. high, branching from near the top or base, terete, striate, sparingly strigose or almost glabrous; leaves opposite below, becoming alternate above, linear, 2-6 cm. long, 1-3 mm. wide, sparingly strigose and resinous punctate, those of the inflorescence shorter and spreading; heads numerous, subsessile on slender branches; phyllaries 4-5, free, obovate, the margins membranaceous and ciliate, resinous punctate, glabrous or strigose on the backs; paleae of the staminate flowers filiform or linear-spatulate, those of the pistillate flowers oblong, truncate to acute at the tip; staminate flowers 5, corolla about 2 mm. long, style about one-half as long as the stamens, stigma capitate, penicillate; pistillate flowers usually 3, corolla about 1 mm. long; achenes brownish when young, black, rugose, and pubescent at the apex when mature, 1-1.5 mm. long. Figures 17-22.

Type not seen.

Distribution: Southern South Carolina, Georgia and Florida.

Representative specimens.—FLORIDA. *Bradford Co.:* Wire grass, long leaf pine sandhills 5 mi. W. of Lee, 7 October 1954, *Godfrey & Murrill 52649* (FSU, G). *Brevard Co.:* Pond in prairie, 26 October 1903, *Fredholm 6161* (G, NY). *Dade Co.:* Pine lands, Everglades, 3 October 1917, *Mosier 187* (US). *Dixie Co.:* Wet peaty ditches, semi-marsh, 10 mi. N. E. of Cross City, 12 October 1957, *Godfrey 56196* (FSU). *Duval Co.:* South Jacksonville, 10 November 1896, *Lighthipe 304* (NY). *Flagler Co.:* 25 June 1942, *West & Arnold* (NY). *Hernando Co.:* Sandy pine woods, vicinity of Brookville, 22 October 1919, *Jones 141* (US). *Jackson Co.:* Wet sands of the field near Lake Seminole, 6 September 1958, *Godfrey 57698* (FSU). *Lee Co.:* Ft. Myers, pineland, 22 September 1916, *Standley 414* (F, G, MOB, NY). *Madison Co.:* Sandy old field along the Suwannee River, 30 January 1955, *Godfrey, Kral & Gillespie 53945* (FSU, G). *Manatee Co.:* Braidentown, 30 September 1900, *Tracy 7103* (F, G, MOB, UC, US). *Osceola Co.:* Edge of pond, 12 October 1903, *Fredholm 6105* (G, MOB, US). *Pasco Co.:* Big Cypress Swamp, 17 October 1925, *O'Neill* (US). *Seminole Co.:* East of Geneva on St. John Road, sandy alluvium of pasture, 10 July 1957, *Kral 5235* (FSU). *Taylor Co.:* Coarse sand, disturbed high pineland about 5 mi. E. of Perry, 9 October 1954, *Godfrey & Morrill 52561* (FSU). *Wakulla Co:* Open sandy pasture 5 mi. S. of Leon County line on state road 69, 30 October 1955, *Kral 1743* (FSU, SMU). GEORGIA. *Charlton Co.:* In low pineland, Folkston, 11 October 1929, *O'Neill 6030* (US). *Dooley Co.:* 3 September 1900, *Harper 579* (G, US). *Jefferson Co.:* 18 September 1897, *Hopkins 50* (NY). *Sumter Co.:* Shaded roadside near Flint River, 10 September 1900, *Harper 629* (G, NY). *Wheeler Co.:* Roadside bordering pineflat, 14 October 1950, *Godfrey 50807* (G, SMU). South Carolina. *Aiken Co.:* 12-15 September 1909, *Eggleston 5069* (F, G, MOB, NY, US).

2. *Iva asperifolia* Less., Linaea 5:151. 1830.

Decumbent perennial, branching from the base and rooting at the nodes; stems 2-4 dm. high, terete, sparingly strigose; leaves 1-2 cm. long, opposite, becoming alternate in the inflorescence, oblong or rarely linear-lanceolate, mostly 1-nerved, obtuse, entire or rarely serrulate, short petioled, sparingly strigose; heads subsessile, solitary in the axils of reduced floral leaves; involucre turbinate, 2-3 mm. broad, about 2.5 mm. high; phyllaries united into a cup, sparingly strigose on the backs, the margins somewhat villous-ciliate; paleae of the staminate flowers linear, those of the pistillate flowers absent; staminate flowers 3-9, corolla about 2 mm. long, style about half as long as the stamens, stigma small and blunt; pistillate flowers 1 or rarely 2 in each head, corolla about 1.5 mm. long; mature achenes usually pubescent at the apex, brown, slightly resin dotted, about 2 mm. long. Figures 23-27.

Type: MEXICO. VERACRUZ. Julio, *Schiede* 332 (G, fragment of type and drawing of the type).

Distribution: Wakulla County, Florida, in the United States, but mostly in the state of Veracruz, Mexico.

The specimens of *I. asperifolia* from Florida may represent an introduction from Mexico. Seeds grown from Florida specimens sent by Dr. R. K. Godfrey were grown in the greenhouse and gave plants with procumbent terms. In Veracruz, Mexico, this species grows on sand dunes directly facing the Gulf of Mexico. Plants on the dunes are decumbent and usually root at the nodes. Some of the specimens collected in Veracruz contained both old and new flowering branches, indicating the perennial nature of the species.

Representative specimens.—UNITED STATES. FLORIDA. Wakulla Co.: banks of brackish marshes, St. Marks, 22 November 1958, *Godfrey 57946* (FSU).

MEXICO. VERACRUZ. Sand dunes facing the Gulf of Mexico at Tecolutla, 22 August 1957, *Jackson 2548* (KANU); sands of seashore, Tampico, 4 July 1896, *Pringle 7293* (G, US); near Veracruz, 18 September 1906, *Rose* & *Rose 11470* (NY, US).

3. *Iva angustifolia* Nutt., DC. Prod. 5:529. 1836.

Annual; stems 5-12 dm. high, branched above, sparingly to densely strigose; leaves opposite below, becoming alternate above. petioled, entire or serrulate, linear-lanceolate, conspicuously 3-nerved on the larger leaves, strigose above and below, 2-4 cm. long, 2-8 mm. wide, those of the inflorescence linear to linear-filiform; heads subsessile in the axils of bracts, involucre turbinate, 2-3 mm. broad, 2-2.8 mm. high; phyllaries united into a cup, strigose to hispid on the backs, villous-ciliate at the tips; paleae subtending the pistillate flowers filiform to linear; those of the pistillate flowers absent; staminate flowers 1-3 in each head, corolla white or pink, about 2 mm. long, style about one-half as long as the stamens and blunt at the tip; pistillate flowers 1 or rarely 2 in each head, corolla about 1.5 mm. long; mature achenes black and rugose, sometimes pubescent at the apex, 2-2.8 mm. long. Figures 28-32.

Type: ARKANSAS. *Nuttall* (NY).

Distribution: Western Arkansas, Oklahoma, Texas and Louisiana.

Representative specimens. — ARKANSAS. *Scott Co.:* Low dry ridges, 30 August 1938, *Demaree 18158* (MOB, NY). *Sebastion Co.:* Massard Prairie, *Armstrong* (TEX). LOUISIANA. *Allen Parish:* 7.2 mi. W. of Kinder, sandy clay, 9 October 1955, *Shinners 22186* (SMU). *Beauregard Parish:* 3 mi. S. of Loganville, sandy ditch, 9 October 1955, *Shinners 22228* (SMU). *Bienville Parish:* Marl of old lime quarry near Friendship, 9 August 1955, *Moore & Wasmer 6460* (G). *Caddo Parish:* 4 mi. N. W. of Greenwood, 6 October 1955, *Shinners 21699* (SMU). *Calcasieu Parish:* Mount prairie area W. of Sulfur, 19 October 1940, *Rogers 8639* (G). *Cameron Parish:* Low prairie, 13 September 1915, *Palmer 8537* (NY, US). *Livingston Parish:* Pineland near Springfield, 18 October 1931, *Brown 3816* (NY). OKLAHOMA. *Craig Co.:* Near Vinita, 18 September 1894, *Bush 288* (MOB, NY). *Creek Co.:* 19 September 1894, *Eggert* (MOB). *Pittsburg Co.:* Sandy prairies, 6 September 1914, *Palmer 6400* (MOB). *Wagoner Co.:* Near Wagoner along open roadside, 10 September 1956, *Jackson 2216* (KANU). TEXAS. *Anderson Co.:* Gus Engeling Wildlife Management Area 6 mi. N. W. of Tennessee Colony, fall 1951, *Marsh 306* (TEX). *Angelina Co.:* 15 August 1934, *Boon* (TEX). *Blanco Co.:* 23 September 1935, *Cory 15732* (G). *Bosque Co.:* Limestone gravel, road shoulder, 23 October 1949, *Shinners 12084* (SMU). *Brazoria Co.:* Vicinity of Houston, 28 January 1913, *Rose 18125* (NY). *Brazos Co.:* College Station, 20 July 1946, *Parks* (TEX). *Burleson Co.:* Sandy-clay fencerow, 13 October 1953, *Shinners 16635* (SMU). *Burnet Co.:* 50 mi. W. of Georgetown, 10-15 October 1879, *Palmer 567* (US). *Cameron Co.:* Brownsville, mouth of the Rio Grande River, 10 August 1924, *Runyon 668* (US). *Comel Co.:* Comanche Springs, New Braunfels, October 1849, *Lindheimer 930* (NY, UC). *Dallas Co.:* chalk slope, 26 September 1948, *Shinners, 10466* (SMU). *Denton Co.:* Gravelly road shoulder, 9 October 1944, *Shinners 11898* (SMU). *Erath Co.:* Limestone hill, 26 September 1950, *Cory 58077* (SMU). *Fayette Co.:* Muldoon, 3 October 1950, *Ripple 51-793* (TEX). *Franklin Co.:* Loose gray sand, road shoulder, 18 September 1953, *Shinners 16249* (SMU). *Freestone Co.:* 15 mi. S. E. of Fairfield, dry sands of bog border, 6 November 1954, *Kral 376* (FSU). *Gillespie Co.:* Williams Creek, *Jermy 684* (US). *Harris Co.:* 10 mi. S. W. Seabrook, 29 August 1943, *Boon* (TEX). *Hays Co.:* San Marcos and vicinity, 1909, *Stanfield* (NY). *Henderson Co.:* Sandy hillside, oak woods, 2 November 1947, *Shinners 9580* (SMU). *Hockley Co.: Thurow 189* (US). *Hood Co.:* Sand, bottom of Rough Creek, 17 September 1948, *Shinners 10358* (SMU). *Hunt Co.:* Sandy-clay soil in drainage ditch, 12 September 1948, *Shinners 10212* (SMU). *Jeff Davis Co.:* Fort Jeff Davis, 19 September 1920, *Eggleston 17374* (NY). *Lamar Co.:* 3.7 mi. S. of Paris, sandy clay soil of old field, 25 September 1953, *Shinners 16332* (SMU). *Liberty Co.:* Sandy soil, 16 October 1930, *Dana 2633* (US). *Madison Co.:* Sandy-clay ditch bank, 9 October 1953, *Shinners 16441* (SMU). *Milam Co.:* Peat bog, 8 November 1941, *Moon 154* (TEX). *Montague Co.:* Gravelly road cut, 1 October 1950, *Shinners 12882* (SMU). *Montgomery Co.:* Sandy drainage way at edge of pine woods, 13 October 1953, *Shinners 16558* (SMU). *Navarro Co.:* Corsicana, dry prairie, 27 September 1902, *Reverchon 3286* (MOB). *Somervill Co.:* Sand and limestone crevices in creek bottom, 19 September 1948, *Shinners 10398* (SMU). *Tarrant Co.:* Open field, 3 October 1910, *Ruth 66* (F). *Travis Co.:* Infrequent on limestone hills 13 mi. S. W. of Austin, 16 October 1944, *Warnock W1058* (TEX). *Trinity Co.:* 5 mi. S. W. of Trinity, 29 September 1934, *Cory 10511* (G). *Van Zandt Co.:* Oak woods, sandy hillside, 19 October 1947, *Shinners 9483* (SMU). *Walker Co.:* Roadside, 9 November 1945, *Cory 50644* (G). *Williamson Co.:* 2.5 mi. N. W. of Hutto on upper Austin Chalks, fall 1945, *Gordon 51-1768* (TEX).

4. *Iva texensis* Jackson, sp. nov.

Planta fruticosa, ad 1.4 *dm. altam; caulibus pluribus (vel unica), supra strigosis, infra levis; foliis subtus oppositis, insuper alternis vel raro oppositis, linearis vel lanceolatis, strigosis cum resinosis punctatis insuper subtusque,* 2-4 *cm. longis,* 3-10 *mm. latis; capitulis in angustis longis frondosis spicatis; involucris turbinatis,* 3-4.1 *mm. longis; phyllariis conjunctis; femineis floribus* 1 *vel raro* 2; *masculinis floribus* 1-5; *achaeniis nigris in maturitate, ca.* 2 *mm. longis.*

Plant shrubby, up to 1.4 dm. high; stems one or several, strigose above, smooth below; leaves opposite below, alternate or rarely opposite above, linear or lanceolate, strigose with resin dots above and below, 2-4 cm. long, 3-10 mm. wide; heads in long, narrow leafy spikes; involucres turbinate, 3-4.1 mm. long; phyllaries united; pistillate flowers 1 or rarely 2; staminate flowers 1-5; achenes black at maturity, about 2 mm. long. Figures 33-37.

Type: TEXAS. *Brooks County:* In saline soil, 8-1 miles south of Falfurrias along U. S. highway 281, August 24, 1957, *Jackson 2505* (KANU). Co-type: *Jackson 2505* (SMU).

Distribution: Coastal area of Texas.

A number of specimens from the coastal region of Texas are tentatively assigned to *I. texensis.* These plants have a rather woody stem, but in involucral length and plant height they are not always in agreement with the type.

Specimens tentatively assigned to I. texensis: TEXAS. *Atascosa Co.:* Pleasanton, 3 October 1917, *Palmer 12924* (TEX). *Cameron Co.:* Clay dunes, Loma de los Patos, August 1957, *Johnston* (TEX). *Galveston Co.:* Galveston Island, 22 August 1901, *Greene 7362* (TEX). *Harris Co.:* Sept.-Oct. 1936, *Anderson 36.2* (TEX). *Kenedy Co.:* Sandy soil, King Ranch, 14 September 1953, *Johnston* (TEX). *Kleberg Co.: Kingsville,* Fall 1940, *Sinclair* (TEX). *Willacy Co.:* Sand at Redfish Bay, 23 November 1953, *Davis* (TEX).

5. *Iva annua* L. var. *annua.*

Iva annua L. Sp. Pl. p. 988. 1753.
Iva ciliata Willd., Sp. Pl. *3:*2396. 1804.
Iva annua Michx., Fl. Bor. Am. *2:*184. 1803.
Ambrosia Pitcheri Torr., Hook. Comp. Bot. Mag. *1:*99. 1835.
Iva ciliata latifolia DC., Prod. *5:*529. 1836.

Coarse annual; stem 4:20 dm. high, angled, hispidulous or hispid; leaves 4-12 cm. long, petioled, serrate, opposite, 3-nerved hispidulous, ovate, or becoming lanceolate above; those of the inflorescence reduced, ovate to broadly lanceolate, entire, hispid, ciliate; heads in elongated spikes terminating the stems and branches; involucre turbinate, 4-5 mm. broad; phyllaries 3-4, free, cuneate, rounded or truncate at the apex, hispid on the backs and hispid-ciliate; paleae of the staminate flowers mostly linear with sessile glands, those of the pistillate flowers filiform or with clavate tips, sometimes lacking; staminate flowers 9-16, corolla about 2.5 mm. long, style about two thirds as long as the stamens, the stigma capitate-penicillate; pistillate flowers 3-5, corollas about 1.5 mm. long; mature achenes 2.5-4.5 mm. long, dark brown, broadly ovate, lenticular, sometimes slightly pubescent at the apex. Figures 38-43.

Type: In the Herbarium of the Linnean Society of London; a photograph of the type has been examined. Botanical drawings of the type are shown in figures 12-16.

Distribution: Maine to Nebraska, south to southwestern Texas and adjacent Mexico, east to Alabama.

Iva annua has gone under the name of its synonym, *I. ciliata* Willd., since the time the latter species was described. This error was probably due to Linnaeus' designation of *I. annua* as "habitat in American meridionali," and a plate by Schmidel (1762) depicting the pistillate flowers of *I. annua* as having 2, 3, or 4 stigma lobes.

Rydberg (1922) was the first American botanist to suggest that *I. annua* might represent an abnormal *I. ciliata* which had been changed through cultivation. To determine the effect of cultivation on *I. annua,* plants were grown in the greenhouse at the University of New Mexico during the winter of 1957. Examination of a number of heads from several plants revealed styles with 2, 3, 4, and occasionally 5 stigma lobes. In all probability, cultivation *per se* was not the cause of deformation. Quite possibly, the day length was the main factor since plants grown outside during the summer produced the normal number of style branches.

Representative specimens.—UNITED STATES. ALABAMA. *Sumter Co.:* Chalky field, 31 October 1937, *Harper 3602* (G, NY, MOB, US). ARKANSAS. *Arkansas Co.:* Rice prairies, 22 September 1940, *Demaree 21667* (F, MOB). *Chicot Co.:* Grand Lake, 4 October 1936, *Demaree 13827* (NY, MOB). *Crittenden Co.:* Valley land, 2 October 1949, *Demaree 28573* (SMU). *Drew Co.:* Margin of swamp, 17 October 1942, *Demaree 24111* (G, NY). *Howard Co.:* Tollette, 7 September 1940, *Moore 400431* (TEX). *Miller Co.:* Along Red River, sandy alluvial soil of cottonwood belt, 26 September 1948, *Whitehouse 20299* (SMU). *Mississippi Co.:* Valley land, 24 September 1948, *Demaree 27450* (SMU). COLORADO. Lat. 61°, 1862, *Hall & Harbour 262* (F). ILLINOIS. *Adams Co.:* 9 September 1917, *Beckwith* (F). *Alexander Co.:* Low ground, 13 October 1950, *Winterringer 5447* (F). *Calhoun Co.:* Kampsville, bottomlands, *Lurnes 1618* (F). *Hancock Co.:* 6 September 1871, *Mead 3451* (MOB). *Lawrence Co.:* Low ground, 16 October 1950, *Winterringer 6197* (F). *Madison Co.:* 7 September 1948, *Demaree 27404* (SMU). *Menard Co.:* Athens, August 1868, *E. Hall* (F). *St. Clair Co.:* Low places, 2 September 1878, *Eggert* (MOB). *Union Co.:* Jonesboro, *Vasey 29-2* (F, G, NY, US). INDIANA. *Gibson Co.:* Hard clay soil along roadside, 3 September 1939, *Deam 59544* (NY). *Posey Co.:* Roadside and waste places near Skeleton, 5 miles south of Mt. Carmel, 2 September 1939, *Kriebel* (PUR). KANSAS. *Allen Co.:* 5 mi. E. of Iola, 5 September 1956, *McGregor 12756* (KANU). *Barton Co.:* Great Bend, 21 August 1884, *Kellerman 1397* (F). *Douglas Co.:* Floodland 1 mi. S. Lawrence, 10 September 1941, *McGregor E.418* (G, SMU, TEX, UC, US). *Jefferson Co.:* Williamstown, wet loam soil in grassland, 30 August 1950, *Latham 656* (KANU). *Jewell Co.:* Floodland along creek, 12 September 1952, *Horr 4401* (G, KANU, NY). *Johnson Co.:* Wet prairie, Olathe, 3 October 1934, *Bush 14221* (MOB). *Kiowa Co.:* Near Belvidere, 26 September 1897, *Ward* (US). *Linn Co.:* La Cygne, 19 September 1934, *Bush 13991* (MOB). *McPherson Co.:* Lindsborg, low ground, August 1888, *Bodin* (F). *Meade Co.:* 8 mi. S. Meade, roadside ditch, 2 September 1951, *McGregor 4048* (KANU). *Reno Co.:* Hutchinson, 5 October 1918, *Benke 2350* (F, US). *Riley Co.:* Wet soil, 31 August 1895, *Morton 255* (G, MOB, NY, US). *Shawnee Co.:* 1 mi. E. Richland, 26 August 1849, *L. D. V. 695* (KANU). *Washington Co.:* Low waste places, 21 October 1916, *Stevens 4339* (NY). LOUISIANA. *Morehouse Parish:* Bottomland, *Demaree 13844* (MOB, NY). *Natchitoches Parish:* Open, dry ground, Natchitoches, 13 September 1915, *Palmer 8727* (MOB, NY). MAINE. *Hancock Co.:* In dump at Bangor, 6 October 1905, *Knight* (G). MASSACHUSETTS. *Suffolk Co.:* S. Boston, 29 September 1878, *Faxon* (G). MICHIGAN. *Wayne Co.:* Near Oakwood salt block, 16 September 1916, *Chandler* (US). MISSOURI. *Bates Co.:* Alluvial excavated ground, Horseshoe Lake, 1 October 1938, *Steyermark 9942* (F). *Chariton Co.:* Bottom meadow in lowlands of Little Clanton River, 16 September 1937, *Steyermark 26451* (F, MOB). *Clay Co.:* Harlam, low ground, 12 September 1897, *McKenzie* (F, NY, MOB). *Franklin Co.:* Allenton, 20 August 1911, *Letterman* (F, US). *Greene Co.:* Willard, 23 August 1893, *Blankenship 737* (US). *Henry Co.:* Bottoms of Grand River, 2 September 1907, *Steyermark* (F). *Jackson Co.:* Along railroads at Kansas City, 13 September 1896, *McKenzie* (NY). Jasper Co.: 16 August 1893, *Bush* (MOB). *Johnson Co.:* Wet, open ground in valley north of Flagstaff Creek, 26 September 1951, *Steyermark 72754* (F). *Knox Co.:* Bottoms prairie, Salt River, 18 September 1950, *Steyermark 70656* (F). *Lafayette Co.:* Wellington, 3 September 1927, *Bush 11515* (MOB). *Linn Co.:* Valley of Locust Creek, Pershing State Park, 26 June 1941, *Steyermark 40451* (F). *Marion Co.:* Deep rich soil, Hannibal, 9 April 1915, *Davis 5194* (MOB). *Mississippi Co.:* Near Morehouse, 3 September 1936, *Rhodes* (G). *Pettis Co.:* Open grassy place around lake, 4 October 1938, *Steyermark 21436* (F). *Ralls Co.:* Along shore of lake formed by salt and sulfur springs, 3 September 1937, *Steyermark 25697* (F, MOB, NY). *St. Charles Co.:* St. Louis, 2 October 1896, *Kellogg* (MOB). *St. Louis Co.:* Broadway and Riverside, 14 July 1939, *Bauer* (F). *Saline Co.:* Low ground along stream near McAllister Springs, 24 August 1934, *Steyermark 14817* (F). *Schyler Co.:* Rich, wooded ravine, 26 August 1950, *Steyermark 70309* (F). *Vernon Co.:* Bottom prairies bordering Stultz Lake, 29 September 1938, *Steyermark 9820* (F). *Webster Co.:* Along the Jordan east of Springfield, 30 August 1911, *Standley 8466.* NEBRASKA. *Buffalo Co.:* Near Kearney, 27 August 1891, *Rydberg 174* (F, NY). *Franklin Co.:* Shores of Thompson Creek, 5 September 1941, *Tolstead 411495* (MOB). *Furnas Co.:* Shores of small pond in Republican Valley, 30 August 1941, *Tolstead 411493* (MOB). *Kearney Co.:* Minden, 2 September 1935, *Hopeman* (MOB, UC). *Lancaster Co.:* Railroad bank, Lincoln, August 1890, *Rydberg* (NY). *Red Willow Co.:* Sandy flood plain, 30 August 1941, *Tolstead 411494* (MOB). NORTH DAKOTA. *Walsh Co.:* Alkaline marsh along road, Lake Ardock, 10 August 1943, *Stevens 746* (MOB, UC). OKLAHOMA. *Cleveland Co.:* Moist river thicket, 17 October 1936, *Hopkins 795* (MOB). *Craig Co.:* Vinita, 18 September 1894, *Bush 286* (NY). *Creek Co.:* Sandy loam soil 2 mi. W. of Sapulpa, 4 October 1946, *Fowler 63* (TEX). *Jackson Co.:* Wet sandy dunes along salt fork of Red River, 3 mi. W. of Altus, 24 October 1936, *Hopkins 1018* (G). *Kingfisher Co.:* Huntsville, 9 October 1896, *Blankenship* (G). *Love Co.:* 16 mi. S. of Marietta, sandy highway hill, Red

River bottoms, 13 October 1950, *Shinners 12912* (SMU). *Oklahoma Co.:* Oklahoma City, September 1944, *Rinkel 2* (F). *Olerie Co.:* Moist river thicket, 17 October 1936, *Hopkins 795* (NY). *Ottawa Co.:* In waste places near Ottawa, 30 August 1913, *Stevens 2463* (G, MOB, NY, US). *Payne Co.:* Loam soil, Stillwater, 19 September 1939, *Harding 260* (MOB). *Pontotoc Co.:* Dry depression along railroad 1 mi. S. of Ada, 17 September 1947, *Robbins 2743* (SMU, UC). *Swanson Co.:* Uncultivated garden, 23 June 1913, *Stevens 1230* (G). *Tulsa Co.:* Black clay soil, 19 September 1942, *Stout 111* (SMU). *Woods Co.:* On creek bank, 5 October 1913, *Stevens 2883* (G). TEXAS. *Aransas Co.:* Aransas refuge, 28 September 1944, *Cory 45780* (TEX). *Archer Co.:* Archer City, 15 September 1934, *Berryman* (NY). *Bastrop Co.:* River bottom and low places, 3 October 1928, *Duval 89* (TEX). *Bexar Co.:* Margin of Mitchel Lake, 9 October 1930, *Clare 400* (UC). *Brazoria Co.:* Columbia, 5 October 1900, *Bush 1285* (MOB). *Calahan Co.:* Draw at roadside, 29 September 1950, *Cory 58395* (SMU). *Cameron Co.:* Rio Grande River bank near international bridge, 10 September 1937, *Runyon 1998* (F). *Clay Co.:* 13 mi. N.E. of Henrietta, 20 October 1942, *Cory 40789* (G). *Collin Co.:* Along highway in yellow clay soil, 18 September 1949, *Turner 1449* (SMU). *Comal Co.:* Weed patch, San Antonio, *898* (NY). *Comanche Co.:* Bottoms of Sabina Creek in seepy area on roadside, 26 September 1955, *Cory 58143* (SMU). *Cooke Co.:* In low places, 30 September 1939, *McCart 1833* (SMU). *Dallas Co.:* Low ground along stream, 28 September 1947, *Shinners 9379* (SMU). *Denton Co.:* Roadside ditches, 18 October 1937, *McCart 686* (F, SMU). *DeWitt Co.:* Western part of county, 1 November 1941, *Riedel* (TEX). *Fayette Co.:* Muldoon, 3 October 1950, *Ripple 51-900* (TEX). *Gonzales Co.:* Palmetto State Park, 18 October 1940, *Tharp* (TEX). *Grayson Co.:* 30 September 1933, *Spinks 6* (MOB, TEX). *Gregg Co.:* 20 October 1937, *York* (MOB, TEX). *Hardman Co.:* Chillicothe, 9 September 1906, *Ball 1130* (US). *Harris Co.:* Clearings adjacent woodlands on Galveston Bay, 26 November 1937, *Shultz 37-31* (F). *Hemphill Co.:* Low ground near Canadian, 11 August 1900, *Eggert* (MOB). *Hidalgo Co.:* Sandy soil, Tobasco, 25 July 1932, *Clover 213* (NY). *Hill Co.:* Yellow silty clay soil, 23 October 1949, *Turner 1697* (SMU). *Hunt Co.:* Sabine River bottoms, 12 September 1948, *Shinners 102322* (SMU). *Jackson Co.:* Buekner, low wet prairie, 5 October 1921, *Bush 9717A* (F, MOB). *McLennan Co.:* Below lake Waco dam on clay bank, 30 September 1947, *Smith 1038* (DAV, TEX). *Montague Co.:* Sandy clay soil along highway, 1 October 1950, *Storm 1129* (SMU). *Parker Co.:* Weatherford, 19 October 1902, *Tracy 8146* (F, G, MOB, NY, TEX, US). *Rockwall Co.:* East fork of Trinity River, 18 September 1946, *Cory 52342* (SMU, UC). *San Patricio Co.:* Roadside ditch, 30 September 1950, *Jones 372* (SMU). *San Saba Co.:* Lowland along creek, 27 September 1950, *Cory 58217* (SMU). *Tarrant Co.:* Borders of "Lake Erie," Handley, 5 October 1920, *Ruth 224* (F, G, NY). *Titus Co.:* Low moist ground, 2 November 1946, *Whitehouse 17746* (SMU). *Travis Co.:* In alluvial soil, Shoal Creek, 9 October 1954, *McCart 4030* (SMU, TEX). *Travis Co.:* Austin, Colorado River floodplain, 10 October 1948, *Tharp 49-1263* (TEX). *Van Zandt Co.:* Bank of stream, 19 October 1947, *Shinners 9500* (SMU). *Walker Co.:* Vacant lot in S. W. Huntsville, 10 November 1945, *Cory 50671* (SMU). *Wheeler Co.:* Flood plain on north fork of Red River, 15 September 1950, *Tharp 51-347* (TEX). *Wichita Co.:* Red River bottoms, 25 September 1944, *Whitehouse 9468* (SMU). *Willbarger Co.:* Low ground near Vernon, 18 September 1903, *Eggert* (MOB).

MEXICO.—TAMAULIPAS. Environs de Matamoros, 1838, *Berlandier 3171* (MOB). TAMPICO. 24 November 1937, *Kenoyer 740* (F).

6. *Iva annua* var. *caudata* (Small) Jackson, comb. nov. *Iva caudata* Small, Bull. N. Y. Bot. Gard. *1*:290. 1899
   Iva annua Lam., Tab. Encyc. *3*:354. 1823.
   Ambrosia Pitcheri β Hook., Comp. Bot. Mag. *1*:100. 1835.
   Iva ciliata β T. & G., Fl. N. Am. 2:287. 1842.

Coarse annual; stem 4-20 dm. high, angled, hispidulous to hispid, or rarely glabrate; leaves petioled, dentate, or sometimes subentire, opposite, 3-nerved, hispidulous, or glabrate on both sides, ovate, or becoming lanceolate above, 3-10 cm. long; those of the inflorescence linear-lanceolate 7-18 mm. long, caudate-acuminate, hispid-ciliate; heads in spikes terminating the stems and branches; involucre turbinate, 4-5 mm. broad, phyllaries 3-4, free, cuneate or truncate, usually hispidulous, ciliate; paleae of the staminate flowers mostly filiform with sessile glands along the margins, those of the pistillate flowers filiform or clavate-tipped; staminate flowers 9-17, corolla about 2.5 mm. long, style about two-thirds as long as the stamens, capitate-penicillate; pistillate flowers 3-5, corollas about 1.5 mm. long, mature achenes 2-4 mm. long, ovate, dark brown. Figure 44.

Type: LOUISIANA. Swamps, September, *Small* (NY).

Distribution: Indiana to Missouri, south to eastern Texas, west along the coastal area of Texas to adjacent Mexico, east to Alabama.

Variety *caudata* is most distinct in Louisiana. In the northern part of its range it becomes somewhat diluted by hybridization with variety *annua.* Although some authors have considered var. *caudata* a habitat modification of the species, specimens from various habitats have been found to remain constant at least for the linear-lanceolate bracts of the inflorescence which seems to be the best diagnostic character of the variety.

Representative specimens.—UNITED STATES. ALABAMA. *Colbert Co.:* Bear Creek, Pickwick Reservoir, 22 September 1945, *Hall* (SMU). *Jefferson Co.:* Roadside ditch, Harper (G, MOB, NY, US). *Mobile Co.:* Mobile, October 1887, *Mohr* (US). *Sumter Co.:* Edge of chalky field, 31 October 1937, *Harper 3602* (NY). ARKANSAS. *Arkansas Co.:* Rice prairie, 22 September 1940, *Demaree 21667* (MOB). *Ashley Co.:* Beech Creek bottoms, 27 September 1937, *Demaree 16372* (NY, MOB). *Clay Co.:* Valley land, 25 August 1939, *Demaree 20316* (MOB, NY). *Crittendon Co.:* Between the levee and Mississippi River, West Memphis, 25 September 1932, *Demaree 9324* (MOB). *Drew Co.:* Margin of swamp, 11 September 1943, *Demaree 24626* (MOB). *Lawrence Co.:* Bottoms, Imboden, 8 September 1951, *Demaree 31337* (TEX). *Phillips Co.:* Helena, Arkansas bottoms, 15 October 1950, *Demaree 30240* (TEX). *Pulaski Co.:* Little Rock, September 1886, (NY). ILLINOIS. *Madison Co.:* Mississippi River bottoms, Collinsville, 7 September 1948, *Demaree 27404* (TEX). *St. Claire Co.:* 2 miles S. of Columbia, 30 September 1956, *Druskel 3059* (MOB). *Union Co.:* Jonesboro, 21 August 1894, *Glatfelter* (G). INDIANA. *Ballard Co.:* High, dry, wooded bank of Turner Lake about 8 mi. N. W. of Bandana, 14 September 1940, *Bacigalupi 60127* (UC). *Posey Co.:* In clay of roadside by Wabash River, 3 September 1939, *Tryon & Tryon 992* (F, FSU, G, MOB, NY, SMU, TEX, UC, US). *Posey Co.:* Waste places at edge of corn field bordering Wabash River, 11 September 1938, *Kriebel 7057* (PUR). *Pulaski Co.:* Jasper-Pulaski Game Preserve, 9 October 1937, *Deam 58587* (IU). *Wells Co.:* Garden, 24 September 1944, *Deam 63137* (IU). LOUISIANA. *Calcasieu Parish:* Lake Charles, 1888, *Davis* (F). *Caldwell Parish:* Damp clay bank above stream, 7 October 1955, *Shinners 21826* (SMU). *Jefferson Parish:* Waste ground along highway, 12 October 1947, *Ewan 17420* (SMU). *Lafayette Parish:* Wet soil at foot of dike, SLI Dairy Farm, ca. 1 mi. S. of Lafayette, 10 September 1957, *Reese*

1393 (FSU). *Natchitoches Parish:* Roadside, silty clay over chalk, 3.5 mi. N. W. Gailbreath, 8 October 1955, *Shinners 22020* (SMU). *Orleans Parish:* New Orleans, 1835, *Ingalls* (NY). *Plaquemines Parish:* In low ground, 14 October 1885, *Langlois* (US). *Rapides Parish:* Fencerow with scattered oaks, sandy-clay soil, 8 October 1955, *Shinners 22053* (SMU). Mississippi. *Copiah Co.:* Bottoms, 21 September 1954, *Demaree 36183* (G). *Jefferson Co.:* Creek bottom, 19 September 1946, *McDougall 1117* (US). *Lamar Co.:* Low ground, Hattiesburg, 16 September 1931, *Sargent* (NY). Missouri. *Marion Co.:* West Hannibal, damp ground, 4 September 1915, *Davis 6287* (MOB). *Pike Co.:* 1880, *Peck* (F). *St. Louis Co.:* River bottoms, St. Louis, 28 September 1893, *Glatfelter* (MOB). Tennessee. *Obion Co.:* Woods near Walnut Log, 19 September 1941, *Eyles 440* (G). Texas. *Cameron Co.:* Southeast part of county, Spring 1942, *Davis* (TEX). *DeWitt Co.:* Yorktown, 28 October 1935, *Parks 17396* (G). *Gonzales Co.* Ottine Swamp, 27 September 1934, *Cory 10115* (G). *Hidalgo Co* Along irrigation ditch, 20 August 1944, *Whitehouse 44258* (G). *Jefferson Co.:* Woods along bayou, 3 October 1945, *Cory 50007* (G, SMU). *Nueces Co.:* River bottom land, 14 October 1954, *Jones 1055* (SMU). *Panola Co.:* Near Carthage, 25 September 1938, *Whitehouse 12093* (SMU). *Willacy Co.:* Raymondville, August 1941, *Shiller 817* (US).

Mexico. Tamaulipas. Matamoros, 1828, *Berlandier 455* (G).

7. *Iva annua* var. *macrocarpa* (Blake) Jackson, comb. nov. *Iva ciliata* var. *macrocarpa* Blake, Rhodora 41:84. 1939.

Phyllaries 3.8-6.5 mm. long, hispid on the backs; paleae of the staminate flowers with sessile glands along the margins; staminate flowers 3.5-4.0 mm. long; achenes 4.8-13 mm. long, 3.2-5.7 mm. wide.

Type: Missouri. *Barry Co.:* Montgomery Rock Shelter, *Dellinger* (US).

This variety has been found only in bluff dwelling sites in Arkansas, Kentucky, and Missouri and probably represents a cultigen derived in a manner similar to *Helianthus annus* var. *macrocarpus* (DC.) Ckll. The achenes are usually larger than any existing races of *I. annua.* The presence of achenes of var. *macrocarpa* in the remains of various bluff dwellings and in the feces of their inhabitants indicate its use as a food and/or medicinal plant (Blake, 1939).

8. *Iva imbricata* Walt., Fl. Car. 232. 1788.
Iva integrifolia Banks, Fl. Am. Sept. 580. 1814.

Perennial, woody at the base; stems decumbent, branched above, up to 10 dm. high, glabrous; leaves 1-5 cm. long, sessile, entire or rarely serrulate, the lowermost opposite, the median and upper ones alternate, oblanceolate to oblong, acute, thick, indistinctly 3-nerved; inflorescence leaves reduced, entire; heads in racemes; involucre hemispheric to campanulate, 5-8 mm. broad, 3.5-5.8 mm. high; phyllaries 6-9, free, imbricate, broadly obovate to orbicular, the margins membranaceous and erose, the backs glabrous; paleae of the staminate flowers spatulate or oblanceolate, erose at the apex, those of the pistillate flowers oblanceolate to elliptic; staminate flowers numerous, corolla 4-6 mm. long, style about two-thirds as long as the stamens, stigma capitate, short-penicillate; pistillate flowers 2-4, corolla 1-1.5 mm. long; achenes 3.5-5.0 mm. long, brown, resin dotted at maturity. Figures 45-49.

Type not seen.

Distribution: Sandy beaches, Virginia to Florida and Louisiana, Bahama Islands, and Cuba.

Representative specimens.—UNITED STATES. ALABAMA. *Baldwin Co.:* Gulf beach, 29 September 1954, *Hildebrand 41* (TEX). *Mobile Co.:* Sandy seashore, Cedar Point, Mobile, July 1869, *Mohr* (US). FLORIDA. *Bay Co.:* On low wet ground about 18″ above water line, St. Andrews Bay, E. end of bridge, 6 August 1958, *Henderson* (FSU). *Brevard Co.:* Cocoa Beach, on coastal sand dunes, 18 August 1957, *Kral 5474* (FSU). *Dade Co.:* Biscayne Bay, 27 April 1920, *Rheder 835* (G). *Duval Co.:* Sandy seashore at mouth of St. Johns River, October 1888, *Curtiss 1399* (F, G, MOB, US). *Escambia Co.:* Dune area near Coast Guard Station on Santa Rose Island, 11 August 1954, *Ford & Arnold 4475* (G). *Gulf Co.:* St. Vincent Island, 1 November 1910, *McAdee 1792* (US). *Hillsborough Co.:* Long Key, west coast, 6 August 1894, *Lewton* (NY). *Lake Volusia Co.:* New Smyrna, 29-31 March 1904, *Burgess 590* (F, NY). *Lee Co.:* On coastal shell ridges, Sanibel Island, 20 July 1954, *Cooley 2295* (G). *Monroe Co.:* Hammocks, Key West, 15-16 November 1912, *Small 3757* (NY). *Orange Co.:* Lake Braully, June 1894, *Leerhn* (F). *Palm Beach Co.:* Sandy shores, August 1929, *Rhodes* (UC). *St. Johns Co.:* St. Augustine, 3 October 1904, *Harrison* (G). *St. Lucie Co.:* East coast, Ft. Pierce, 8-9 April 1904. *Burgess 712* (F). GEORGIA. *Chatham Co.:* Tybee Island, sand dunes, 29 September 1900, *Harper 733* (NY, US). *Glynn Co.:* Side of sandy ridge near beach on Sea Island, 21 August 1950, *Duncan 11841* (G, MOB, SMU). LOUISIANA. *Jefferson Parish:* Grand Island, 18 October 1954, *Hildebrand 76* (TEX). *Orleans Parish:* New Orleans, *Ingalls* (NY). *St. Bernard Parish:* Breton Island, 17 August 1900, *Tracy* & *Lloyd 491* (F, G, MOB, NY, US). MISSISSIPPI. *Harrison Co.:* Deer Island off Biloxi, 2 October 1898, *Tracy 4733* (F, MOB, NY). *Jackson Co.:* Sand near the coast of Round Island, 13 August 1953, *Demaree 33732* (FSU). NORTH CAROLINA. *Brunswick Co.:* Sand dunes, Ft. Caswell, 18 October 1940, *Radford 699* (UC). *Cataret Co.:* Atlantic Beach, dune, 1 September 1938, *Godfrey 6491* (G, US). *Columbus Co.:* Whiteville, dunes, 6 August 1911, *Hashberger* (NY). *Dare Co.:* Lee side of dunes ca. 5 mi. N. of Rodanthe, 13 September 1955, *Wilbur 5052* (G). *New Hanover Co.:* Carolina Beach, dune, 27 August 1938, *Godfrey 6182* (G, US). SOUTH CAROLINA. *Beaufort Co.:* Bluffton, November 1875, *Mellichcamp* (MOB, NY). *Charleston Co.:* James Island, Charleston, November 1875, *Mellichcamp* (MOB). VIRGINIA. *Norfolk Co.:* Near Ocean View, 20 July 1898, *Kearney 1752* (US). *Princess Anne Co.:* Sand dunes, Virginia Beach, 3-19 September 1905, *McKenzie 1722* (G, MOB, NY).

BAHAMA ISLANDS. Andros Island; sandy sea shore, Kemp Bay, 9-17 August 1906, *Brose 5029* (F, NY). New Providence Island; sea beach, Delaport, 26 August 1904, *Britton* & *Brace 305* (F, NY). Inagua Island; strand, south shore, 14 October 1904, *Nash* & *Taylor 1040* (F, NY).

CUBA. Camaguey. Cayo Paredon Grande, 25 October 1909, *Schafer 2769* (F, G, NY). *Habana.* Seashore, June 1819, *Leon 8919* (NY).

9. *Iva frutescens* L. ssp. *frutescens*
Iva frutescens L. Sp. Pl. 989. 1753.

Shrubby perennial; stems 1-3.5 m. high, strigose above, glabrous below; leaves 4-9.5 cm. long, opposite, becoming alternate in the inflorescence, serrulate with usually 5-9 teeth on each side, narrowly lanceolate to lanceolate, 3-nerved, strigose above and below, 5-8 times as long as broad; inflorescence leaves linear, mostly entire; heads numerous in leafy panicles; involucre hemispheric, 4-5 mm. broad, 2-3 mm. high; phyllaries 4-5, free, obovate or oval, sparingly strigulose on the backs; paleae of the staminate flowers narrowly spatulate to oblanceolate; those of the pistillate flowers broadly spatulate or elliptic; staminate flowers 6-19, corolla about 2 mm.

long, style two-thirds as long as the stamens, stigma capitate and short-penicillate; pistillate flowers 4-5, rarely 6, corolla about 1 mm. long; mature achenes brown, resin dotted, 1-2.5 mm. long. Figures 50-54.

Type not seen. A photograph of the type (KANU) has been studied. The type specimen is in the Linnean Society Herbarium in London.

Distribution: Coastal area of the United States from Virginia to Florida and Texas.

Representative specimens.—ALABAMA. *Mobile Co.:* Seashore, July 1868, *Mohr* (US). FLORIDA. *Brevard Co.:* Titusville, July 1895, *Nash 2287* (F, G, MOB, NY, US). *Dade Co.:* Virginia Key, upper part of Biscayne Bay, 27 October 1906, *Small* & *Carter* (NY). *Duval Co.:* Brackish shores near Jacksonville, September 1888, *Curtiss 1396* (F, G, NY, US). *Gulf Co.:* Saline marshes, Apalachiola, Aug.-Sept. 1897, *Chapman 2585B* (NY). *Hillsborough Co.:* Sandy sea beach, 9 September 1904, *Fredholm 6373* (G, MOB, US). *Lee Co.:* Occasional in scrub bordering mangrove swamp, Bokeelia Island, 31 December 1957, *Godfrey 3904* (FSU). *Manatee Co.:* Along Manatee River, 22 September 1932, *West* (UC). *Pasco Co.:* Near Gulf of Mexico, 7 September 1925, *O'Neill 1186* (G). *St. John Co.:* Border of salt marsh, St. Augustine, 20 September 1898, *Curtiss 6457* (G, MOB, NY, US). *Taylor Co.:* Upper margin of salt marsh, 16 August 1957, *Godfrey 55951e* (FSU). *Volusia Co.: Baker 550* (G). *Wakulla Co.:* Beach, S. W. of Panacea near mouth of river, 14 August 1954, *Ford* & *Arnold 4672* (G). GEORGIA. *Chatham Co.:* Margin of salt marsh, 28 September 1900, *Harper 727* (NY, US). LOUISIANA. *Cameron Parish:* Vicinity of Cameron, 29 November 1910, *McAtee 1920* (US). *New Orleans Parish:* New Orleans, 29 July 1916, *Fisher 166* (US). *Terrebonne Parish:* Brackish marshes and bayou banks, Point a Barro, 13 August 1912, *Wurzlow* (NY). MISSISSIPPI. *Hancock Co.:* Tidal marsh about 1 mi. S. of Clairmont Harbour, Gulfport, 10 August 1952, *Channell 1520* (SMU). *Harrison Co.:* Deer Island, off the coast, 3 August 1896, *Pollard 1183* (G, MOB, NY, US). *Jackson Co.:* Low areas near coast, 19 August 1949, *Demaree 28255* (SMU). NORTH CAROLINA. *Brunswick Co.:* Sand with some shell, waterfront, Southport, 29 September 1941, *Godfrey 10058* (TEX). *Carteret Co.:* Sandy soil along the road, 19 August 1949, *Culberson* (UC). *Dare Co.:* Hatteras Island, frequent along border of sandy woods, outskirts of Buxton, ca. 12 mi. N. E. of Hatteras, 13 September 1955, *Wilbur 5026* (FSU, G).

New Hanover Co.: River shore, 27 August 1938, *Godfrey 6186* (G, US). *Onslow Co.:* Bear Inlet, 22 July 1919, *Harris C19553* (US). SOUTH CAROLINA. *Beaufort Co.:* Marsh near Hardner's Corner, 14 August 1939, *Godfrey* & *Tryon 1543* (G, NY, US). *Georgetown Co.:* Cat Island, Georgetown, 16 August 1915, *Alexander 120* (US). *Jasper Co.:* Good Hope Camp, Ridgeland, 11 September 1915, *Alexander 281* (US). TEXAS. *Brazoria Co.:* Chocolate Bayou, September 1943 (MOB). *Calhoun Co.:* At edge of water in sand at Port Lavaca, 4 August 1946, *Gentry 58* (TEX). *Galveston Co.:* Galveston Island, 25 August 1957, *Jackson 2533* (KANU). *Harris Co.:* Goose Creek, *Means* (TEX). *Jackson Co.:* Lavaca River, 24 August 1941, *Tharp* (G). *Jefferson Co.:* N. W. of Sabine Pass, 4 September 1934, *Cory 19889* (G). *San Patricio Co.:* 8 mi. S. of Taft in saline soil along Nueces Bay, 28 June 1951, *Jones 580* (SMU). VIRGINIA. *Lancaster Co.:* Saltmarsh Hollow, windmill point, 15 September 1951, *Smith 5560* (US). *New Kent Co.:* Saltmarsh by York River, 13 October 1939, *Fernald* & *Long 11634* (G, MOB). *North Hampton Co.:* Border of salt marsh, 13 October 1935, *Fernald* & *Long 5553* (G). *Princess Anne Co.:* Fresh to brackish swamp along Landing River, near Creeds, 9 September 1935, *Fernald* & *Long 5120* (G). *Surry Co.:* Sandy beach at mouth of James River, 17 September 1938, *Fernald* & *Long 9476* (G). *York Co.:* Near Newport News, shrub in moist sand, 17 August 1936, *Bartley* & *Pontius 5321* (NY).

10. *Iva frutescens* subsp. *oraria* (Bartlett) Jackson, comb. nov.
Iva oraria Bartlett, Rhodora 8:26. 1906.
Iva frutescens var. *oraria* (Bartlett) Fern. & Griscom, Rhodora 37:184. 1935.

Shrubby perennial; stems 5-1.2 dm. high, striate-angled, strigulose above, usually glabrous below; leaves 4-12 cm. long, opposite below, petioled, elliptic to obovate, serrate with usually 8-17 teeth on each side, thick, 3-nerved, strigose on both surfaces, about 2.5-4 time as long as broad; inflorescence leaves linear-lanceolate, usually entire; heads numerous in leafy panicles; involucre hemispheric, 4.5-6 mm. broad, 2.3-4.5 mm. high; phyllaries 5-6, free, ovate, sparingly strigulose on the backs; paleae of the staminate flowers linear, those of the pistillate flowers oblanceolate or oblong; staminate flowers 6-19, corolla about 2 mm. long, style about two-thirds as long as the stamens, stigma capitate, short-penicillate; pistillate flowers 5-6, corolla about 1 mm. long; mature achenes brown and resin dotted, 2.0-3.9 mm. long. Figures 55-59.

Type: MASSACHUSETTS. *Suffolk Co.:* banks of the Charles River, Boston, 18 September 1905, *Bartlett 293* (NY). Isotype: (US).

Distribution: Eastern coast of the United States and Canada from Nova Scotia to North Carolina. One specimen has been collected as far south as Georgia, and several plants near Galveston, Texas. The Texas specimens may represent introductions by way of shipping cargos from the east coast.

There is some evidence of intergradation of ssp. *oraria* and *frutescens* in the vicinity of Virginia as Fernald and Griscom have pointed out. However, to the north and south of this area the two entities are quite distinct. Measurements of specimens chosen at random from throughout their ranges yielded the data given in Table II.

TABLE II. Measurements of various characters of ssp. *oraria* and ssp. *frutescens*. Linear measurements are in millimeters.

Subspecies	Characters measured	Mean	Range	Number plants examined
oraria	Phyllary length	3.1	2.3–4.5	34
	Achene length	2.5	1.9–3.9	27
	Number teeth per leaf side	11.0	8–17	27
	Length of teeth	1.7	0.6–3.7	27
frutescens	Phyllary length	2.3	2–3	28
	Achene length	2.0	1.6–2.2	23
	Number teeth per leaf side	6.1	5–8	29
	Length of teeth	0.6	0.2–1.3	28

Although there is overlapping for most of the characters, the more northern ssp. *oraria* is somewhat larger than *frutescens*. In all probability, the two subspecies hybridize occasionally where their ranges come together. However, in view of the several demonstrable differences between the two entities, the term subspecies seems to more nearly fit their evolutionary stage of divergence rather than a varietal epithet.

Representative specimens.—UNITED STATES. *Connecticut. Fairfield Co.:* 8 August 1889, *Drew* (UC). *Haven Co.:* East Haven, 1886, *Wenton* (G). *New London Co.:* Seashore, Groton, 8 August 1929, *Gaussman* (TEX). DELAWARE. *Kent Co.:* Along Murderkill Creek, 13 October 1933, *Larsen* (MOB). *New Castle Co.:* Collins Beach, June 1863, *Canby* (NY). *Sussex Co.:* Wet hollows in sand dunes, 29 August 1936, *Fogg 11350* (G). GEORGIA. *Chatham Co.:* Salt marsh, 28 September 1900, *Harper 727* (US). MARYLAND. *Anne Arundel Co.:* Wet sandy east bank of Severn River, 1¼ mile N.E. of Annapolis, 9 October 1938, *Herman 9995* (US). *Calvert Co.:* Chesapeake Beach, 25 August 1918, *Hunnewell 5577* (G). *Charles Co.:* Salt marsh, 2 September 1954, *Sargent 7062* (SMU). *Dorchester Co.:* Swamp near Cambridge, 16 August 1904, *House 234* (NY). *St. Marys Co.:* Between Piney Point and Millstone, 3-4 September 1911, *Liedstrom 5270* (US). *Talbot Co.:* Margin of W. shore of Chesapeake Bay, 17 September 1939, *Allard 7424* (US). MASSACHUSETTS. *Barnstable Co.:* Coulit, 28 August 1912, *Jack* (G). *Bristol Co.:* Sandy seashore, Westport, 29 September 1929, *Churchill* (MOB). *Dukes Co.:* Traps Pond, salt marsh, 23 July 1935, Seymour *1004a* (G. SMU). *Essex Co.:* Newberry, 1892, *Oaks* (MOB). *Middlesex Co.:* Malden, 13 September 1876, *Morong* (MOB). *Nantucket Co.:* Nantucket Island, pond by east of harbor, 29 August 1904, *Bicknell* (NY). *Norfolk Co.:* Dorchester, 1871, *Churchill* (MOB). *Plymouth Co.:* Wareham, along tidal marsh, 6 June 1906, *Baxter* (UC). *Plymouth Co.:* Salt marshes, Nantusket, 21 September 1916, *Blake 6569* (US). *Suffolk Co.:* Banks of the Charles River, Boston, 18 September 1905, *Bartlett 293* (F, G, MOB, NY (type), MOB, TEX, UC, US). NEW JERSEY. *Atlantic Co.:* New Gretna, salt marsh, *Killip* (US). *Burlington Co.:* Salt marsh, Baso River, 31 August 1937, *E. T. & H. N. Moldenke 10196* (MOB, NY). *Cape May Co.:* 28 September 1929, *Albertto* (NY). *Cumberland Co.:* Open brackish marsh, Perry Island, 26 August 1933, *Adams 1121* (G). *Monmouth Co.:* Redbank, 3 September 1923, *Beals* (NY). *Ocean Co.:* On sand beaches along inlet back of Point Pleasant, 17 August 1940, *Bright 17896* (TEX). *Salem Co.:* Island in brackish marsh about 3 mi. S of Hancock's Bridge, 3 October 1935, *J. W. & M. T. Adams 2482* (G, MOB). *Somerset Co.:* Woodbridge, 3 September 1894, *Lighthipe* (MOB). NEW YORK. *Nassau Co.:* Long Beach, Long Island, 15 August 1909, *Bicknell 8165* (NY). *Queens Co.:* Rockaway Park, 7 September 1901, *George* (NY). *Richmond Co.:* Vicinity of New Darp, Stanton Island, 2 August 1890, *Small* (F). *Suffolk* Co.: Wading River, L. I., 24 September 1923, *Ferguson 2632* (NY). *Westchester Co.:* Border of marsh, north Tarrytown, 2 October 1895, *Barnhardt 1262* (NY). NORTH CAROLINA. *Dare Co.:* 21 September 1940, *Stewart 869* (UC). *Hanover Co.:* 4 June 1911, *Bartlett 2550* (US). RHODE ISLAND. *Kent Co.:* Liverton, August

1879, *Sargent 250* (G). *Providence Co.:* Providence, 20 August 1878, *Congdon* (MOB). Texas. *Galveston Co.:* Galveston, 18 September 1877, *Ward* (MOB). Virginia. *Accomack Co.:* Saline swamp, Pocomoke River, August 1897, *Rothrock* (F). *Prince George Co.:* Shore of Monroe Bay near Colonial Beach, 2 August 1912, *Tiedstrom 5943* (US). *Middlesex Co.:* Sandy brackish marsh, 10 September 1939, *Fosberg 16741* (FSU, NY, US). *Nansemond Co.:* Tidal shore of Nansemound River, 18 September 1937, *Fernald & Long 7702* (G). *Norfolk Co.:* Near Lafayette River, Norfolk, 9 September 1944, *Hubrecht B2690* (MOB). *North Hampton Co.:* Cape Charles City, 25 September 1894, *Canby & Rose 812* (US). *Princess Anne Co.:* Tidal marsh, Cape Henry, 3 September 1940, *Eggler 40-366* (NY). *Surrey Co.:* Hog Island, fresh to brackish tiday marshes, 26 August 1940, *Fernald & Long 12880* (G, US). *Westmoreland Co.:* Salt marshes, Lynch Point, summer 1941, *Iltis 882* (SMU). *York Co.:* Scimino Creek at York River, low sandy flat along creek, 8 October 1921, *Grimes 4569* (NY).

Canada. *Nova Scotia. Hants Co.:* Salt marshes, 30 August 1945, *Dore 451110* (G, US).

11. *Iva cheiranthifolia* H. B. K., Nov. Gen. & Sp. 4:276. 1820.

Shrubby perennial; stems 1-2 m. high, striate-angled, strigose above, glabrous below; leaves entire, petioled, opposite except in the inflorescence, linear-lanceolate to oblanceolate, 3-nerved, acute or sometimes obtuse, 4-8 cm. long, up to 2.5 cm. wide; inflorescence leaves, linear or linear-lanceolate; heads numerous in leafy panicles; involucre hemispheric, 3-4 mm. broad, about 2.5 mm. high; phyllaries 3-5, free, slightly imbricate, obovate or orbicular, very obtuse, the margins somewhat membranaceous; paleae of the staminate flowers spatulate, those of the pistillate flowers broadly oblanceolate to elliptic; staminate flowers 5-16, corolla about 2.5 mm. long, style about half as long as the stamens, stigma capitate, short-penicillate; pistillate flowers 3-5, corolla about 1 mm. long; achenes obovate, brownish, resin dotted about 2 mm. long. Figures 60-64.

Type not seen. A photograph of the type (KANU, F, US) has been examined.

Distribution: Bahama Islands, Cuba, and possibly Florida.

The single nonflowering specimen of *I. cheiranthifolia* labeled "Florida" is the only one known from the U. S. This may have been brought into Florida by chance or the specimen label may have been incorrect.

Representative specimens.—BAHAMA ISLANDS. *Andros Island:* Coppice near Deep Creek, Long Bay Cay Section, 20-27 January 1910, *Small* & *Carter 8593* (F, NY). *Berry Islands:* Edge of mangrove swamp, Whale Cay, 29 January 1905, *Britton* & *Millspaugh 2194* (F, NY). *Grand Island:* Pine barrens, 1888, *Eggers* (F, G). *New Providence Island:* S.W. beach, February 1926, *J.* & *A. R. Northrop 311* (F, NY). *North Bimini Islands:* 16 April 1904, *Millspaugh 2372* (F).

CUBA. *Camaguey.* Gonado, Cayo Sabinal, 17-18 March 1909, *Schafer 881* (F, G, US). *Habana.* Bank of creek near Guanabacoa, 27 January 1905, *Curtiss 620* (F, MOB, US); Mariano, coastal plains, 22 February 1910, *Britton* & *Wilson 4503* (NY); near Habana, 1860-64, *Wright 2847* (G). *Ila de Pinos.* Siguanea, coastal sands, 26 February 1916, *Britton* & *Wilson 14941* (F, NY); beach west of Punta de Bibijagua, 28 April 1951, *Killip 41280* (US); Playa de Herradiera, 21 March 1953, *Killip 4315* (US). *Pinar Del Rio.* Bahia Hando, rocky places near coast, 14 December 1910, *Wilson 9268* (NY). *Las Villas.* Saline soil, 22 July 1929, *Jack 7534* (F, G, G); District of Cienfuegos, 13 August 1895, *Combs 453* (F, G, MOB, NY).

UNITED STATES. FLORIDA. 1842-49, *Rugel 95* (MOB).

12. *Iva hayesiana* A. Gray, Proc. Am. Acad. 11:78. 1876.

Shrubby perennial; stems up to 1 m. high, strigose above, glabrous below; leaves opposite, becoming alternate in the inflorescence, short-petioled, entire, or rarely with 1-3 uneven teeth on one side, broadly oblanceolate to spatulate, obtuse, strigose to scabrescent, 3-6 cm. long; heads numerous in leafy racemes or sometimes the lower ones in short panicles; involucre hemispheric, 5-6 mm. broad, about 3 mm. high; phyllaries 5-6, free, obovate, strigose on the backs; paleae of the staminate flowers spatulate; those of the pistillate flowers spatulate to elliptic; staminate flowers 8-20, corolla 1.5-2.0 mm. long, style about two-thirds as long as the stamens, stigma subcapitate, penicillate; pistillate flowers usually 5, or sometimes 6, corolla 0.5-1.0 mm. long; mature achenes brown, resin dotted 1.9-2.3 mm. long. Figures 65-69.

Type: CALIFORNIA. *San Diego Co.:* Jamuel Valley, 1875, *Palmer 160* (NY).

Distribution: Southern California and Baja California.

Representative specimens.—UNITED STATES. CALIFORNIA. *San Diego Co.:* Tijuana, 30 June 1884, *Orcutt* (G, MOB); Tijuana

River, Lia Tijuana, 14 May 1903, *Abrams 3514* (MOB, NY); San Carlos River, 10 September 1923, *Eastwood 12424* (G).

MEXICO. *Baja California.* Ceders Island, July-October 1896, *Anthony 41* (F, G, MOB, UC, NY); Ensenada to Guadalupe, 24 May 1936, *Bailey 516* (F); Socorro, 22 July 1889, *Brandagee* (UC); San Ysidro, 28 June 1894, *Schoewfelt 3814* (US); dry ravines between Tomas and San Jacinto, 7 September 1930, *Wiggins & Demaree 4727* (F, G, UC, US); banks of small stream at Valencia Beach, between Halfway House and Alisitos, 10 September 1929, *Wiggins & Gillespie 3941* (F, G, MOB, US).

13. *Iva axillaris* Pursh, Fl. Am. Sept. 743. 1814.
Iva foliosa Nutt., Trans. Am. Phil. Soc. II. 7:346. 1840.
Iva axillaris pubescens A. Gray, Bot. U.S. Expl. *17*:350. 1874.
Iva axillaris normalis Kuntz, Rev. Gen. *1*:348. 1891.
Iva axillaris brevifolia Kuntz, Rev. Gen. *1*:348. 1891.
Iva axillaris linearifolia Kuntz, Rev. Gen. *1*:348. 1891.
Iva obovata Greene ex. C. F. Baker, West. Am. Plants *1*:18. 1902.
Iva axillaris Robustior Hook, Fl. Bor. Bor.-Am. *1*:309. 1834.

Perennial with creeping rootstocks, herbaceous or woody at the base; stems ascending, 3-6 dm. high, striate, strigose to sparingly villous; leaves subsessile, entire, opposite below, becoming alternate above, ovate, elliptic or sometimes spatulate, obtuse and indistinctly 3-nerved, glabrate to rather densely pubescent on both surfaces; leaves of the inflorescence smaller, but similar to the main leaves; heads short, peduncled, solitary in the axils of the floral leaves; involucre hemispheric, 4-5 mm. broad, about 2.5-3.0 mm. high; phyllaries 4-5, united to the middle or above to form a cup, or rarely one phyllary free, the tips rounded, glabrous to strigose on the backs; paleae of the staminate flowers oblanceolate to almost spatulate, those of the pistillate flowers oblanceolate or sometimes absent; staminate flowers 8-20, corolla 2-2.5 mm. long, style about two-thirds as long as the stamens, stigma capitate, short-penicillate; pistillate flowers 5-8, corolla about .5 mm. long; mature achenes brownish, resin dotted, 2.5-3 mm. long. Figures 70-74.

Type not seen.

Distribution: Nebraska north to Manitoba in Canada, west to Alberta, southwest to Washington, Oregon, and California, and east to New Mexico.

The rhizomatous growth habit of *I. axillaris* appears to be a unique characteristic of the genus and may represent a mechanism for rapid propagation of relatively minor variations over rather large areas. Two chromosome numbers have been reported for the species, and a triploid population was found in New Mexico. The triploid plants were growing near the banks of the San Juan river and were widely spaced. Although cytological material was taken from several widely separated plants, all were triploid and rather highly pollen sterile. This, perhaps, indicates the value of the rhizomatous habit of the species as a mean of vegetative reproduction.

The more notable morphological variations of the species are in pubescence, leaf shape, and degree of phyllary union. Specimens from the same geographic area may be glabrate or have long loose hairs (as in var. *pubescens* Gray). Kuntze named several varieties according to leaf shape, but these types can sometimes be found in the same population. The degree of phyllary union varies throughout the range of the species. However, specimens with one phyllary free and four united have occurred more frequently in specimens from the northern part of the species range. Nevertheless these variations do not, in my opinion, warrant taxonomic recognition since they are more or less sporadic throughout the range of the species.

Representative specimens.—UNITED STATES. ARIZONA. *Coconino Co.:* Painted Desert, Tuba Oasis, cultivated ground, 15-31 July 1920, *Clute 56* (G, MOB, NY). CALIFORNIA. *Alamedo Co.:* Livermore, April 1892, *Beoletti* (UC). *Contra Costa Co.:* 20 May 1930, *Halperin* (DAV). *Eldorado Co.:* On Lincoln Highway, 5 mi. E. of Kyburg, 11 September 1915, *Heller 12270* (DAV, F, G, MOB, NY, UC). *Inyo Co.:* West side of Westguard Pass, 14 June 1956, *Raven 6997* (NY). *Kern Co.:* Scodie Meadows, Kernville, 2 October 1931, *Lewis* (UC). *Lassen Co.:* 26 August 1910, *Eggleston 6208* (US). *Modoc Co.:* Goose Lake Valley, July 1895, *Austin 143* (US) & *234* (UC). *Mojave Co.:* Victorsville, roadside, *Munz, Harwood* & *Johnston 4073* (UC). *Mono Co.:* In alkaline ground among *Chrysothamnus*, 5 July 1944, *Alexander* & *Kellog 3813* (MOB, TEX). *Monterey Co.:* Dry, rain pool, 5 July 1936, *Rose 32225* (MOB, US). *Moore Co.:* Ft. Bidwell, 1903, *Manning 20* (US). *Nevada Co.: Truckee*, 10 August 1886, *Sonne 369* (F, UC). *Orange Co.:* Crushed gravel in dry road bed, 16 June 1943, *Paddock 12732* (NY). *Placer Co.:* Blue Canyon, 4701 ft., 23 June 1908, *Walker 1217* (UC). *Riverside Co.:* Dry heavy soil at woodside, 3 July 1918, *Johnston 2014* (UC). *San Bernadino Co.:* Quartzite debris, Gold Mt. above Baldwin Lake, 19 June 1932, *Fosberg 8582* (MOB). *San Diego Co.: Mission Valley,* 6 October 1940, *Cans* (UC). *Santa Barbara Co.:* Guadalupe, 29 July 1908, *Condit* (UC). *Sierra Co.:* 1874, *Lemmon* (NY). *Shasta Co.:* 6 mi. S. of Fall River Mills, 3800 ft., June 1903, *Hall & Babcock 4260* (UC). *Siskiyou Co.:* Saline flat near lower Klamath Lake, 12 September 1910, *Butler 1874* (MOB, UC, US). *Solano Co.:* Southern Pacific R.R. tracks at Cordelia, 10 July 1947, *Heiser 1959* (UC). *Ventura Co.:* Griffen's, July 1902, *Elmer 3592* (F, MOB, NY). Westroba *Co.:* 21 September 1920 (DAV). COLORADO. *Adam Co.:* Denver, damp alkaline soil, 12 August 1910, *Eastwood 33* (UC, US). *Boulder Co.:* Roadside, 5 mi. S. of Longmont, *K. M. & M. C. Wiegand 2538* (G). *Gunnison Co.:* Gunnison, 1896, *Clements 111* (NY). *Kiowa Co.:* Clayey slopes at reservoir between Lamar and Eads, 4000 ft., 4 May 1947, *Porter 4129* (G, SMU, TEX). *Larimer Co.:* Ft. Collins, 8 July 1898, *Crandall 3268* (Tex, US). *Mesa Co.:* Grand Junction, 11 June 1901, *Baker 110* (G, MOB, NY, UC, US). *Moffat Co.:* Elk Spring, 6800 ft., 28 July 1933, *Herman 5326* (G, MOB). *Morrison Co.:* 18 June 1891, *Smith* (MOB). *Weld Co.:* Evans, 1909, *Johnson 101* (MOB). IDAHO. *Ada Co.:* Open hillside, Boise, 14 September 1911, *Clark 331* (F, MOB, NY, UC, US). *Bear Lake Co.:* Dry, open flat of Douglas fir zone, St. Charles Canyon, 23 July 1952, *Baker 9546* (NY). *Blaine Co.:* Overgrazed flat in Oregon Gulch, 6300 ft., 29 July 1941, *Cronquist 3490* (G, MOB). *Butte Co.:* Cultivated field at edge of desert, 14 June 1941, *Cronquist 2388* (G, MOB). *Canyon Co.:* Valley, Falk's Store, 22 June 1910, *McBride 276* (NY, UC, US). *Cassia Co.:* Roadside wasteground, 2 mi. N. E. of Elba, 29 August 1951, *Baker 8778* (NY). *Clark Co.:* Along R. R. tracks 2 mi. S. of Duboise, 16 August 1937, *Cronquist 1929* (MOB). *Custer Co.:* Sagebrush flats 10 mi. W. of Clayton, 5 August 1944, *Hitchcock & Muhlich 10773* (SMU, UC). *Elmore Co.:* Dry banks above river, Atlanta, Boise Nat'l Forest, 18 September 1942, *McFadden 25347* (G, TEX). *Franklin Co.:* Roadside waste ground, Cache Valley, 13 July 1952, *Baker 9259* (NY). *Owyhee Co.:* Roadsides & slopes, 14 July 1910, *McBride 288* (F, MOB, NY, UC, US). *Power Co.:* 5 mi. W. of Pocatello in salty, marshy meadow, 12 July 1937, *Christ 8368* (NY). *Twin Falls Co.:* McCullen Creek, 26 June 1937, *Christ & Ward 8028* (NY). MONTANA. *Cascade Co.:* Great Falls, September 1885, *Anderson 4069* (NY). *Dawson Co.:* Colgate near Glendive, 6 September 1892, *Sandberg 1015* (G, NY, US). *Gal-*

latin Co.: Bozeman and vicinity, 19 August 1905, *Blankinship 278* (F, MOB). *Lewis & Clark Co.:* Helena, 7 July 1891, *Kellog* (F, MOB). *Madison Co.:* 28 July 1947, *Hitchcock 16937* (UC). *Meagher Co.:* Near Centerville, July 1883, *Scribner 102* (US). *Park Co.:* 1901, *Scheuber 98* (NY). *Sheridan Co.:* Westby, 21 June 1927, *Larsen 51* (MOB). NEBRASKA. *Lancaster Co.:* Lincoln, 3 August 1900, *Hedgerk* (MOB). *Scotts Bluff Co.:* Near Platte, 23 July 1891, *Rydberg 175* (NY, US). *Sioux Co.:* Orella, 6 July 1912, *Pool & Folson* (MOB). NEVADA. *Eureka Co.:* Eureka, 7000 ft., 29 June 1941, *Raynor* (DAV). *Churchill Co.:* Roadside, 8 July 1937, *Allen 303* (RENO). *Clark Co.:* Along R. R. track, 16 August 1939 (RENO). *Elko Co.:* Along Humboldt River, 29 September 1937, *Train 550* (RENO). *Lander Co.:* Moist ravine, vicinity of Austin, 26 July 1913, *Hitchcock 713* (US). *Lincoln Co.:* Canyon floor, pinyon-juniper belt, 19 August 1935, Hall (RENO). *Lyon Co.:* Wet clay, sand soil, 500 yds. N. of Wellington, 23 June 1937, *Lehenbauer 154* (MOB, RENO). *Mineral Co.:* W. side of Walker Lake, 16 September 1938, *Archer 7137* (RENO, UC). *Nye Co.:* Along U.S. hwy. 50, 20 July 1937, *Goodner & Henning 811* (RENO). *Ormsby Co.:* Kings Canyon, 1700-2000 ft., 10 July 1902, *Baker 1310* (G, US). *Storey Co.:* 6300 ft., open, dry places, 9 September 1937, *Allen 519* (RENO). *Washoe Co.:* Streets and vacant lots of Reno, 27 September 1937, *Archer 5730* (RENO, SMU). *White Pines Co.:* Near stream, 12 mi. N. E. of Ely, 17 August 1938, *Hitchcock 4656* (G). NEW MEXICO. *Rio Arriba Co.:* Opposite San Juan, 5675 ft., 24 June 1897, *A. A. & E. G. Heller 3764* (G, MOB, NY, US). *San Juan Co.:* Vicinity of Farmington, dry fields, 17 July 1911, *Standley 6890* (US). *San Miguel Co.:* Las Vegas to Arriba, 16 June 1924, *Eggleston 20128* (F, NY). *Socorro Co.:* Beside the Rio Grande, 3 mi. N. of Socorro, 25 July 1925, *Wiegand & Upton 4440* (F, MOB). NORTH DAKOTA. *Barnes Co.:* Hillside, Valley City, 27 June 1950, *Stevens* (US). *Benson Co.:* Leeds, 21 July 1901, *Lunnell 5587* (G). *Carson Co.:* Saline soil, 30 July 1915, *Over 3448* (US). *Stark Co.:* On Clay Butte, Belfield, 21 June 1912, *Stevens & Waldron* (G). *Williams Co.:* Williston, 14 August 1891, *Bolley* (NY). OREGON. *Clark Co.:* Portland, 16 July 1902, *Sheldon S10611* (F, G, MOB, NY, US). *Crook Co.:* Between Prineville & Farewell Bend, 20 July 1894, *Leiberg 484* (UC, US). *Gilliam Co.:* Arlington, in dry fields and rocky places, 25 August 1903, *Mell 257* (US). *Grant Co.:* Alkaline flats, 23 June 1925, *Henderson 5233* (G). *Harney Co.:* Dry ditch banks along the roadside in flats, 4600 ft., 30 July 1953, *Cronquist 7668* (NY, SMU). *Jefferson Co.:* Dry roadside on W. side of Deschutes River, 5 August 1955, *French 1606* (NY). *Klamath Co.:* Moist alkaline ground, 6 July 1920, *Peck 9347* (G, MOB). *Lake Co.:* Near Button Springs, 23 August 1894, *Leiberg 789* (G, MOB, NY, UC, US). *Sherman Co.:* Bottoms near river mouth, 25 May 1925, *Henderson 5234* (G, MOB). *Union Co.:* Union, 21 June 1904, *Hunter 565* (US). *Wallowa Co.:* Jim Creek, 1425 ft., 15 June 1897, *Sheldon 8300* (F, G, MOB, NY, UC). *Wasco Co.:* Deschutes Canyon near Manpin, 28 May 1933, *Peck 17354* (NY). SOUTH DAKOTA. *Harding Co.:* Moist places in prairie, 22 July 1920, *Over 11335* (NY). *Washington Co.:* Sandy valleys, 23 July 1914, *Rydberg 2149* (MOB). UTAH. *Beaver Co.:* 6,000 ft., Fisco, 26 June 1930, *Keck 636* (G, UC). *Box Elder Co.:* Saline flats, Bear River Refuge, 23 September 1936, *Piranian 14858* (UC). *Cache Co.:* July 1890, *Glatfelter 250* (MOB). *Garfield Co.:* Panguitch, 2-5 September 1912, *Eggleston 8133* (RENO). *Iron Co.:* 8 mi. N. Cedar City, 27 July 1927, *Harris N27125* (MOB). *Juab Co.:* Nephi, Exp. Farm., *Ball 1773* (US). *Piute Co.:* Along Sevier River, Marysvale, 19 July 1905, *Rydberg* & *Carlton 6449* (G). *Rich Co.:* 1873, *Budge* (US). *Salt Lake Co.:* Murroy, 17 July 1917, *Jones 510* (G). *San Pete Co.:* 25 July 1914, *Eggleston 10262* (US). *Servier Co.:* Level loam soil, 5 July 1940, *Bishop 9MB* (NY). *Uintah Co.:* West side of Green River, 20 mi. S. of Vernal, 4700 ft., 18 June 1931, *Graham 6092* (G). *Utah Co.:* Provo, 25 June 1894, *Jones 5505a* (US). WASHINGTON. Washtucna, June 1898, *Elmer 1038* (US). *Chelan Co.:* Leavenworth, 27 August 1901, *Umback* (US). *Douglas Co.:* Jct. Crab & Wilson Creeks, 27 June 1893, *Sandberg* & *Leiberg 318* (F, G, MOB, NY, UC). *Grant Co.:* In damp soil at S. end of the lake, August 1943, *Eyerdam 6378* (SMU, UC). *Okanogan Co.:* Along bank of Robinson Creek, 10 August 1937, *W. C.* & *M. W. Muenscher 11198* (G). *Whitman Co.:* Sandy soil, Indiana, 20 May 1923, *St. John* & *Warren 3394* (MOB, NY). WYOMING. *Albany Co.:* On loose banks, 16 July 1900, *Nelson 7595* (G, US). *Big Horn Co.:* Dry, alkali land east of Manderson, 6 July 1921, *Dann* & *Douglas 2621* (MOB). *Carbon Co.:* Dry sandy plains and rocky hills, July 1901, *Tweedy 4030* (US). *Fremont Co.:* Gustav Lake, 8 August 1947, *Beetle 4947* (UC). *Natrona Co.:* Waste ground, 5100 ft., 7 July 1933, *Herman 4594* (MOB). *Park Co.:* Ditch bank, Cody, 10 September 1913, *County Agent* (UC). *Platte Co.:* Wheatland, 14 July 1894, *Nelson 476* (MOB). *Sheridan Co.:* Dayton, September 1899, *Tweedy 2042* (NY). *Sweetwater Co.:* Granger, grass lands along river, 27 August 1930, *Hanna 646* (MOB).

CANADA. *Alberta.* Arid soil, vicinity of Calgary, 18 July 1894, *Moodie 30* (MOB); alkaline marsh, Rosedale Trail, 24 July 1915, *Moodie 1117* (NY); Bear Lake, near Grand Prairie, Peace River District, 11 September 1939, *Groh 892* (UC). *Manitoba.* Sauris Plains, Macoun (US); along the line of the Grand Trunk Pacific Railway, 20 June 1906, *Macoun* & *Harriot 43024* (F, NY). *Saskatchewan.* Alkaline flat, 4 mi. W. of Humboldt, 26 June 1941, *Breitung 1176* (UC); roadside, Silton, 8 August 1913, *Johnson 1267* (NY); Lethbridge, 5 June 1894, Macoun 5048 (MOB); Moose Jaw, 22 June 1907, *Cowles 60* (F, MOB); Assinboia, 5 June 1894, *Macoun 5048* (G).

14. *Iva acerosa* (Nutt.) Jackson, comb. nov.
Oxytenia acerosa Nutt., Jour. Acad. Phila. II. *1*:172. 1848.

Perennial; stems 1-8 mm. high, terete, striate-angled, strigose above, glabrous below; leaves alternate, pinnatifid with 3-7 linear-filiform divisions, strigose, 5-10 cm. long; heads numerous in terminal panicles; involucre hemispheric, about 5 mm. broad, 3-4 mm. high; phyllaries 5, distinct, ovate-acuminate, the backs somewhat sereccious; paleae of the staminate flowers spatulate with villous backs; those of the pistillate flowers elliptic, oblanceolate, or sometimes vestigial, densely villous; staminate flowers 9-22, corolla about 2.5 mm. long, style almost as long as the stamens, stigma capitate-penicillate; pistillate flowers usually 5, corolla absent, fleshy disc present at the base of the style; mature achenes brownish and long villous, 2-2.5 mm. long. Figures 75-80.

Type not seen.

Distribution: Southern Colorado, northern New Mexico, Utah, Arizona, and southeastern California.

Although this species is the type of the monotypic genus *Oxytenia* proposed by Nuttall, I can see no reason for considering it generically distinct from *Iva*. The narrowly linear to filiform divisions of the leaves apparently impressed Nuttall very much as the name *Oxytenia acerosa* implies. However, within the section Cyclachaena most of the species have leaves that are dissected, and the linear lobes of *I. acerosa* merely represents a further divergence.

Iva acerosa appears to be more closely related to *I. xanthifolia* and *I. nevadensis* than other species in the section Cyclachaena. This is apparent in phyllary, paleae, and pubescence characters.

All three species have phyllaries that are somewhat caudate or acuminate, and the trichomes of *I. nevadensis* and *I. acerosa* are quite similar. A further likeness of the two latter species is the presence of shortened and rather rounded stigma lobes. The small disc at the base of the style inside the pistillate corollas of *I. nevadensis* and *I. xanthifolia* may be represented in *I. acerosa* by the so-called fleshy ring at the base of the style which some authors have considered as a vestigial corolla.

Representative specimens.—ARIZONA. *Navajo Co.:* Kayenta, Painted Desert, 7-12 July 1920, *Clute 8* (G, MOB). CALIFORNIA. *Inyo Co.:* Telescope Mt., S. E. California, 1871, *Wheeler* (G). COLORADO. *Mesa Co.:* Claylike soil at foot of steep canyon of the Colorado River, 5500 ft., 16 August 1937, *Rollins 1938* (G, MOB). NEW MEXICO. *Sandoval Co.:* Bernalillo, alluvial soil, 14 August 1957, *Jackson 2506* (KANU). UTAH. Dry stream bed along U. S. hwy. 53, 16 August 1934, *McGuire* & *Richards 13377* (G). *San Juan Co.:* Lime Creek, 5 mi. N. of Mexican Hat, 24 July 1939, *Cutler 2700* (MOB). *Uintah Co.:* Creek bed, Chandler Canyon, 2 August 1935, *Graham* (G).

15. *Iva dealbata* A. Gray, Pl. Wright. *1*:104. 1852.
Leuciva dealbata (A. Gray) Rydberg, Fl. N. A. *33*:8. 1922.

Perennial; stems erect, 3-7 dm. high, striate-angled, tomentose; leaves petioled, alternate, oblanceolate in outline, pinnately cleft and veined, the terminal divisions ovate or oblanceolate, the basal divisions usually lanceolate, rugose-tomentose above and below, 5-12 cm. long; heads in numerous terminal panicles; involucre hemispheric, about 3 mm. broad; phyllaries 5, distinct, slightly imbricate, ovate, the margins membranaceous and villous-ciliate, usually glabrous on the backs; paleae of the staminate flowers absent, vestigial, or rarely well developed and oblanceolate; those of the pistillate flowers rarely present; staminate flowers 7-14, corolla about 1.5 mm. long, style about as long as the corolla tube, frequently with two well developed stigma lobes, or sometimes the two lobes fused on one side and penicillate; pistillate flowers usually 5, corolla 0.3-0.7 mm. long; achenes dark brown or purplish at maturity, 1.4-2.0 mm. long. Figures 81-84.

Type: From W. Texas to El Paso, New Mexico, May-Oct. 1849, *Wright 317* (G). Isotype (US).

Distribution: New Mexico, south to the states of Durango, Zacatecas, San Luis Potosi, and Nuevo Leon in Mexico, east to western Texas.

This species was described as an annual and has been considered as such by most authors. However, transplant studies have shown that this species is a true perennial.

Representative specimens.—UNITED STATES. NEW MEXICO. *Hidalgo Co.:* Hatchita Plains, 12 September 1902, *Davidson 727* (G). *Lincoln Co.:* White Mts., 5400 ft., 21 July 1897, *Wooton 188* (G, NY, UC, US). *Otero Co.:* White Sands, 28 August 1897, *Wooton* (G, US). *Sierra Co.:* Kingston, gravelly flat, 6600 ft., 13 October 1904, *Metcalf 1490* (G, NY, UC, US). *Socorro Co.:* Socorro, 5 October 1919, *Eggleston 16232* (US). TEXAS. *Brewster Co.:* 13 mi. N. E. of Alpine, 29 October 1935, *Cory 17521* (G). *Culberson Co.:* In ditch, 16 June 1943, *Waterfall 4551* (G, NY). *Hudspeth Co.:* Sierra Blanca, 6 September 1925, *Berkman 3811* (TEX). *Jeff Davis Co.:* In grassland 45 mi. N. E. of Van Horn, 4100 ft., 14 September 1940, *Shreve 9997* (FSU, UC). *Pecos Co.:* 4¼ mi. N. E. of Hovey, 29 October 1935, *Cory 17518* (G). *Presidio Co.:* Fisher Ranch, ditch, 21 August 1941, *Henckley 2116* (G, US).

MEXICO. *Chihuahua.* Laguna de los Patos, October 1852, *Thurber 792* (G, NY); El Carmen, 10 October 1935, *LeSueur Mex. 324* (F, G, TEX, UC); plains near Chihuahua, 4 October 1885, *Pringle 280* (G, NY, US); valley of Jimenez, 5500 ft., 23 October 1905, *Pringle 13560* (G, US); clay valley near Ciudad Juarez, *Stern 194* (NY); Candelaria, 24 October 1911, *Sterns 224* (US); between Casas Grande and Sabinal, 4-5 September 1899, *Nelson 6364* (G, US). *Coahuila.* Saltillo, July 1898, *Palmer 150* (G, NY, UC, US); Soledad, a section of low Mts. with few oaks, 25 mi. S. W. from Monclova, 9-19 September 1880, *Palmer 737* (US); 3 mi. S. of La Ventura, 12 September 1938, *Johnston 7623* (G); Sierra de Pino, vicinity of La Moria, 20-26 August 1940, *Johnston* & *Muller 682* (G); base of mountains along E. margin of Valle de Acatita, 21 September 1942, *Santos 2710* (G). *Durango.* Grama grassland, 18-2,000 ft., 19-20 September 1948, *Gentry 8352* (G, UC, US). *Nuevo Leon.* Foot of Silla Mts., Monterrey, 2 October 1923, *Kenoyer* (MOB). *San Luis Potosi.* Characas, July-August 1934, *Lunndell 5605* (US). *Zacatecas.* 22 mi. S. of Conception del Oro in low ground, 23 September 1938, *Johnston 7356* (G).

16. *Iva Nevadensis* M. E. Jones, Am. Nat. *17*:973. 1883. *Chorisiva nevadensis* (M. E. Jones) Rydb. N. Am. Fl. *33*:9. 1922.

Diffusely branched, pubescent-stemmed annual, up to 4 dm. tall; leaves 1-2 cm. long, pinnately-cleft, the lobes ovate or obovate, obtuse; heads solitary, usually scattered throughout the leafy inflorescense, frequently subtended by small leaves; involucre hemispheric, about 3 mm. broad; phyllaries 3, canescent, caudate with rather large, obovate appendages; paleae of the staminate flowers linear to filiform; those of the pistillate flowers broadly orbicular, ciliate; staminate flowers 8-10, corolla about 2 mm. long, villous-pubescent, style about two-thirds as long as the stamens, stigma capitate, penicillate; pistillate flowers usually 3 in each head, corolla about 2 mm. long, villous-pubscent; stigma lobes short and thick, style with a small disc at the base, achenes about 2 mm. long, somewhat compressed, obovate, the inner face tubercled, the outer slightly so, black at maturity. Figures 85-90.

Type: NEVADA. *Mineral Co.:* Hawthorne, 23 June 1892, *M. E. Jones 4071* (NY).

Distribution: Western Nevada and adjacent California.

Representative specimens.—CALIFORNIA. *Mono Co.:* Mono-Inyo County line between Bishop and Benton, 30 June 1936, *Kerr 4* (UC). NEVADA. *Esmeralda Co.:* Dry desert valley, 20 June 1932, *Duran 3325* (G, UC, US). *Lander Co.:* Dry sandy soil, 13 September 1937, *Henning 95* (MOB). *Lincoln Co.:* 10 mi. E. of Groom Lake on road to Crystal Springs, volcanic ash, 27 August 1938, *Train 2384* (UC). *Mineral Co.:* Hawthorne, 23 June 1882, *M. E. Jones 4071* (NY, UC). *Lyon Co.:* Sandy wash, Pine Grove Hills, 21 June 1947, *Alexander 5320* (UC). *Nye Co.:* 5 mi. S. E. of Tonopah, 11 August 1917, *Hall 10540* (UC).

17. *Iva xanthifolia* Nutt., Gen. Pl. 2:185. 1818.
    Cyclachaena xanthifolia (Nutt.) Fresen., Ind. Sem. Hort. Frankf. 4. 1836.
    Iva paniculata Nutt., Trans. Am. Phil. Soc. II. 7:347. 1840.
    Euphrosyne xanthifolia A. Gray, Pl. Wright. 2:85. 1853.
    Cyclachaena xanthifolia var. *minor* Waura, Stin. Princ. S. Coburg. 2:40. 1888.
    Cyclachaena pedicellata Rydb., Fl. N. Am. I. 33:10. 1933.
    Iva pedicellata (Rydb.) Cory, Rhodora 38:407. 1936.
    Iva xanthifolia var. *pedicellata* (Rydb.) Kittel, Fl. Arizona and New Mexico, 425. 1941.

Coarse annual; stem 0.4-2.0 m. high, usually glabrous but sometimes pubescent; median leaves opposite, 7-30 cm. long, 3-nerved, usually scabrous above, strigose or tomentose below, ovate or subcordate, coarsely serrate and sometimes 3- to 5-lobed; heads numerous in axillary spikes or panicles and terminal naked panicles, sessile or pedunculate; involucre turbinate, 4-5 mm. broad; phyllaries 5, obovate acuminate, hispid on the backs; paleae of the staminate flowers subulate or filiform but sometimes absent in the center of the receptacle; those of the pistillate flowers obovate, concave, ciliate; staminate flowers 8-20, corolla about 2.5 mm. long, style about two-thirds as long as the stamens, the stigma peltate; pistillate flowers usually 5, corolla 0.5 mm. long or represented only by a small disc at the base of the style; mature achenes obovate, finely muricate, usually dark brown, about 3 mm. long. Figures 91-95.

Type not seen.

Iva xanthifolia was probably native to the western United States originally, but it has spread throughout the U. S. and to Europe as a weed.

Distribution: Quebec to Alberta in Canada, south to Arizona, New Mexico, and Texas, east to Maryland. Introduced to various European countries.

Representative specimens.—UNITED STATES. ARIZONA. *Hawthorne Co.:* Near Granado, 18 October 1903, *Griffiths 5820* (US). COLORADO. *Arapahoe Co.:* Denver, 11 September 1910, *Eastwood 126* (G, UC, US). *Boulder Co.:* 6 mi. S. W. of Boulder, dry sandy soil along edges of roadside park, 24 August 1956, *Wagenknecht 2965* (KANU). *Douglas Co.:* Dry creek near Golden, 1 August 1881, *Ward* (US). *El Paso Co.:* Colorado Springs, 1908, *Pace 439* (MOB). *Huerfano Co.:* Near Gardener, sandy creek bottom, 7000 ft., 10 September 1900, *Vreeland 662* (NY). *Jefferson Co.:* Mountain meadow at edge of field near Bergen Park, 14 August 1941, *Waterfall 3443* (G). *La Plata Co.:* Near Durango, 10 August 1904, *Wooton 2594* (US). *Laramie Co.:* Ft. Collins, 7 September 1895, *Cowen* (NY, US). *Los Animas Co.:* Stonewall, August 1917, *Beckwith 255* (UC). *Montrose Co.:* Moist river bottom, Naturita, 14 September 1912, *Walker 546* (G, US). *Pueblo Co.:* Pueblo, September 1883, *Woodward* (G). *Summit Co.:* Roadsides, Green Mt. Falls, 26 September 1917, *Young* (TEX). CONNECTICUT. *Fairfield Co.:* Waste ground, Bridgeport, 9 August 1907, *Cames 5744* (G, NY). *New Haven Co.:* Nangatuck, 19 July 1908, *Blewitt* (G). DISTRICT OF COLUMBIA. Georgetown, vacant lot at Pennsylvania & 34th St., 9 August 1920, *Freeman* (US). IDAHO. *Ada Co.:* On ditch bank, 27 August 1937, *Christ & Ward 8806* (NY). *Blaine Co.:* Dry ground along Carey Lake, 29 August 1952, *Baker 9995* (NY). *Butte Co.:* Little Lost River near Howe, 10 August 1895, *Henderson* (US). *Canyon Co.:* Caldwell, 28 August 1932, *Christ 6418* (NY). *Cassia Co.:* Waste ground along road, 24 August 1951, *Baker 8692* (NY). *Clark Co.:* Cultivated fields, Spencer, 10 July 1916, *Christ 2868* (NY). *Custer Co.:* Along highway just N. of Mackay, 13 August 1941, *Cronquist 3826* (G). *Lincoln Co.:* Shoshone, 20 August 1893, *Palmer 510* (US). *Twin Falls Co.:* Twin & Shoshone Falls, loamy river bottom, 27 July 1911, *Nelson* & *McBride 1374* (G, UC). ILLINOIS. *Champaign Co.:* Along railroad, Urbana, 17 September 1949, *Ahles 1703* (TEX). *Cook Co.:* 14 September 1940, *Mills 192* (NY). *Menard Co.:* "From seed," 1886, *Hall* (NY). *Tazewell Co.:* Waste ground, 27 August 1949, *Chase 10771* (F). INDIANA. *Tippecanoe Co.:* Along railroad tracks ½ mile E. of drive to Purdue Univ. Airport, summer 1952, *Smith* (PUR). IOWA. *Boone Co.:* The Ledges, 15 August 1937, *Pammel* (UC). *Chickasaw Co.:* New Hampton, 1890, *Rolfs* (MOB). *Clay Co.:* Bare place in Deweys Pasture, 9 September 1941, (MOB). *Dickenson Co.:* Prairie, August 1901, *Shimek* (MOB). *Dubuque Co.:* Dubuque, 18 August 1923, *Benke 3738* (F). *Emmet Co.:* Waste places, August 1890, *Cratly* (UC, US). *Fremont Co.:* Waste places, 15 June 1898, *Fitzpatrick 13530* (F, G). *Kossuth Co.:* 28 August 1897, *Pammel 608* (G, MOB). *Woodbury Co.:* Sioux City, September 1909, *Campbell 53* (G, MOB). KANSAS. *Cheyenne Co.:* 10 mi. S. W. St. Francis, sand flood plains along Republican River, 27 August 1957, *McGregor 13560* (KANU). *Douglas Co.:* Lawrence, 28 August 1884, *Oyster 4062* (KANU). *Gove Co.:* 12 mi. S. of Gove, rock-ridge prairie, 29 August 1957, *McGregor 13657* (KANU). *Hamilton Co.:* 22 June 1912, *Wilson* & *Miller* (KANU). *Hodgeman Co.:* Clay soil, roadside ditch, 5 September 1949, *McGregor 3982* (KANU). *Miami Co.:* Paola, August 1886, *Oyster* (MOB). *Morton Co.:* Bank of Cimarron River on alluvial deposit, 27 August 1951, *McGregor 5159* (KANU). *Riley Co.:* Manhattan, August 1892, *Thompson* (NY). *Rooks Co.:* Rockport, 28 August 1889, *Bartholomew* (MOB). *Saline Co.:* Near Bavaria, 15 September 1946, *Hancin 758* (KANU). *Wallace Co.:* 2 mi. E. Sharon Springs, sandy flats along Smoky Hill River, 28 August 1957, *McGregor 13823* (KANU). *Wyandotte Co.:* Armourdale, 12 September 1895, *McKenzie* (NY). MAINE. *Cumberland Co.:* Greenley's henyard, Cumberland, introduced with feed, 21 August 1909, *Chamberlain 1279* (US). *Oxford Co.:* East of Livermore, 20 August 1908, *Parlin 2727* (G). *Sagadahoc Co.:* Brunswick, 17

September 1907, *Furbish* (G). MASSACHUSETTS. *Nantucket Co.:* Nantucket Island, old wharf, 5 September 1904, *Bicknell* (NY). *Norfolk Co.:* Milton, henyard, 12 October 1909, *Margesson* (G). *Suffolk Co.:* Brookline St., Cambridge, vacant lot, 20 August 1910, *Williams* (G, US). MICHIGAN. *Emmet Co.:* in millyard at Pellston, *Colburn* & *Dean 212* (MOB). *Keweenau Co.:* Near coal house, August 1889, *Farwell 619* (G, NY). *St. Claire Co.:* Port Huron, back yard, 6 September 1908, *Dodge 61* (G). MINNESOTA. *Carlton Co.:* Duluth, sand dunes, 31 August 1936, *Lakela 1821* (NY, US). *Cass Co.:* Middle of beach of S. shore of Luck Lake, 5 September 1940, *Moore* & *Butters 13517* (G). *Wabasha Co.:* Lake City, 19 August 1883 (G). *Ramsey Co.:* St. Paul, 1861, *Hale* (G, MOB). *Winona Co.:* September 1905, *Hilzinger* (NY). MISSOURI. *Buchanan Co.:* Alluvial soil along Sugar Lake, 3 mi. E. of Hutchinson, 4 September 1934, *Steyermark 15204* (G, MOB). *Jackson Co.:* Kansas City, 15 September 1924, *Durnam* (TEX). *Lincoln Co.:* Whiteside, August 1931, *Lewis* (MOB). *Broadwater Co.:* Roadside, 16 August 1945, *Hitchcock* & *Muhlveck 13656* (NY). MONTANA. *Gallatin Co.:* Bozeman, 2 September 1902, *Jones* (G, UC). *Lewis* & *Clark Co.:* Helena, *Carleton 234* (F). *Missoula Co.:* Missoula, roadside, 16 August 1925, *Kirkwood 2140* (UC). *Sweet Grass Co.: Greycliff,* 27-30 August 1913, *Eggleston 9918* (US). NEBRASKA. *Custer Co.:* Moist spots N. W. of Broken Bow, 4 September 1927, *Dietz* (G). *Grant Co.:* In the Lake Region, *Rydberg 1783* (G, NY, US). *Kearney Co.:* Minden, 25 August 1932, *Hapeman* (SMU, TEX). *Keith Co.:* South Platte River, flood-plain among willows, 7 September 1943, *Kiener 15331* (G). *Keya Paha Co.:* Meadowville, Cub Creek, 25 August 1898, *Clements 2909* (US). *Knox Co.:* In Niobrara River valley on banks of swamp, 25 August 1936, *Tolstead 710* (G). *Lancaster Co.:* Lincoln, 7 September 1887, *Webber* (NY). *Otoe Co.:* Nebraska City, 1889, *Williams* (US). *Scotts Bluff Co.:* 25 August 1901, *Baker* (MOB). *Thomas Co.:* Old field near Thedford, 7 September 1893, *Rydberg 1740* (NY, US). NEVADA. *Elko Co.:* Moist loam soil, roadside, *Holmgren 2018* (UC, NY). *Mineral Co.:* Rocky gravel soil, 10 September 1938, *Archer 7024* (RENO). NEW HAMPSHIRE. *Hillboro Co.:* Petersborough, weed in garden, 2 September 1928, *Batchelder* (MOB). NEW JERSEY. *Cape May Co.:* Capeway City, 12 October 1935, *Witte* (NY). *Essex Co.:* East Orange, 9 September 1915, *Lighthipe* (NY, TEX). *Hunterdon Co.:* About buildings, 20 July 1913, *Fisher* (NY). NEW

MEXICO. *Bernalillo Co.:* Tree Springs, Sandia Mts., 8200 ft., 29 September 1956, *Jackson 2732* (KANU). *Colfax Co.:* 21 September 1907, *deForesta* (UNM). *Mora Co.:* Bottomland near Mora River, 17 August 1947, *Fendler* (MOB). *Rio Arriba Co.:* Chama, September 1899, *Baker 689* (G, NY). *Sandoval Co.:* Cuba, 24 August 1903, *Castetter 579* (UNM). *San Juan Co.:* Vicinity of Ceder Hill, 17 August 1911, *Standley 8049* (US). *San Miguel Co.:* Vicinity of Las Vegas, 16 October 1876, *Arsene 7652* (MOB). *Taos Co.:* Taos, 7 September 1929, *Whitehouse* (TEX). NEW YORK. *Albany Co.:* Railroads, Albany, 8 August 1923, *House 9583* (G). *Columbia Co.:* Barnyard near Chatham, 24 August 1934, *Muencher* & *Clausen 4765* (US). *Erie Co.:* Buffalo, 7 August 1944, *Knoblock 30042* (G). *Onondago Co.:* Roadside and wet places S. E. corner of Onondaga Lake, 21 August 1916, *Wiegand 7283* (G). *Queens Co.:* Queens, L. I., 1 September 1936, *Monachino 154* (SMU, TEX, US). *St. Lawrence Co.:* Farm yard, Massena Center, 5 September 1930, *Muencher* & *Maguire 1453* (G, US). *Saratoga Co.:* Yard of abandoned house, 28 August 1918, *Burnham* (G). *Ulster Co.:* Pasture, 18 August 1948, *Moldenke* (SMU). NORTH DAKOTA. *Benson Co.:* Waste places, Leeds, 29 October 1901, *Lunnel* (G). *Cass Co.:* Fargo roadside, 19 August 1940, *Stevens 486* (MOB, UC). *Morton Co.:* Mandan, 1915, *Sarvis 145* (US). OHIO. *Geauga Co.:* Parkman Twsp., farmyard, 26 September 1924, *Webb 1618* (G). *Pickaway Co.:* At the stockyard in Circleville, 30 August 1947, *Pontius* & *Bartley 1047* (US). OKLAHOMA. *Blaine Co.:* Sand of floodplains of the N. Canadian River, 3 mi. W. of Watongo, 18 August 1940, *Waterfall 2385* (G). *Ellis Co.:* Rich, waste places by creek near Shattuck, 11 October 1913, *Stevens 2954* (G, MOB, NY, US). *Payne Co.:* Sandy soil river, Perkins, 25 September 1936, *Sooter 93* (TEX). *Texas Co.:* Goodwell, 24 August 1940, *Jamasson* (MOB). OREGON. *Jackson Co.:* Grants Pass, 17 October 1939, *Beals* (TEX). *Union Co.:* Grand Round Valley, 1882, *Cusick 1025* (G). SOUTH DAKOTA. *Brookings Co.:* S. D. A. C. Campus, 29 August 1903, *Johnston* (MOB). *Custer Co.:* 19 August 1892, *Rydberg 797* (NY). *Harding Co.:* Slim Buttes, 19 August 1910, *Visher 137* (F). *Lawrence Co.:* Waste ground, Deadwood, 14 August 1910, *Murdock 4318* (G). TEXAS. *Hall Co.:* About 8 mi. W. of Estelline on Prairie Dog Town fork of Red River, sandy flats along river, 6 September 1945, *Whitehouse 10750* (SMU, TEX, UC). *Hemphill Co.:* 2 mi. N. E. of Canadian, 28 September 1935, *Cory 16260* (G). *Randall*

Co.: West of Amarillo, 14 October 1907, *Ball 1270* (UC, US). *Wheeler Co.:* Floodplains, N. fork of Red River, 15 September 1950, *Tharp 51-343* (TEX). UTAH. *Box Elder Co.:* Bear River Refuge, 1935, *Lehman 29* (TEX). *Cache Co.:* Depot, 19 September 1909, *Smith 2080* (F). *Morgan Co.: Ogden,* 25 August 1910, *Eggleston 6193* (US). *Piute Co.:* Marysvale, 6500 ft., 21 August 1894, *Jones 5848* (NY, MOB, UC). *Salt Lake Co.:* Salt Lake City, 26 August 1879, *Jones 1340* (F, G, NY). *San Pete Co.:* Gunnison, 5050 ft., 2 September 1875, *Ward 675* (MOB, US). *Uintah Co.:* Along irrigation ditch, 5300 ft., 4 September 1931, *Graham 7437* (G, MOB). WASHINGTON. *Chelan Co.:* Along railroad, Wenatchee, 26 August 1901, *Umback* (NY). *Klickitat Co.:* Bottomlands of the Columbia River, September-October 1884, *Sukodorf 355* (G). *Spokane Co.:* Spokane, 17 August 1892, *Sandberry 919* (US). WISCONSIN. *Lincoln Co.:* In an alley of Tomahawk, 23 August 1950, *Seymour 12157* (SMU). *Milwaukee Co.:* Railroad siding, 17 September 1940, *Shinners 3297* (UC). WYOMING. *Albany Co.:* Waste ground, 15 August 1900, *Nelson 7654* (G, MOB, NY, US). *Johnson Co.:* Buffalo, September 1900, *Tweedy 3131* (NY). *Sheridan Co.:* Stream bed, September 1899, *Tweedy 2040* (NY). *Teton Co.:* Dry soil, Hot Spring Bar, 15 mi. S. of Jackson, 19 July 1901, *Merril* & *Wilcox 954* (G, US).

CANADA. *Alberta.* Roadside and waste places, Carlston, 12 August 1914, *Moodie 24* (US); Strome, side of railroad, 4 August 1926, *Brinkman 2521* (US). *Manitoba.* Portage la Prairie, 15 September 1906, *Macoun* & *Herriot 73026* (G). *Ontario.* Great Lakes Region, 27 August 1911, *Dodge* (TEX). *Quebec.* Ottawa, Wenham, Peace Road district, 14 September 1939, *Groh 985* (UC); Montreal, 29 August 1934, *Marie-Victorin* & *Rolland-Germain 43825* (G). *Saskatchewan.* Plains, 31 August 1872, *Macoun 946* (G).

ROMANIA. In ruderal areas about Basarabia District, Iasi, 13 September 1935, *Arvat 1568* (US).

GERMANY. *Bavaria,* Ludwigshafen, an der westichen Hofenstrasse, September 1904, *Poeverlein 824* (G).

18. *Iva ambrosiaefolia* A. Gray subsp. *ambrosiaefolia.*
    Iva ambrosiaefolia A. Gray Syn. Fl. N. Am. *1(2)*:246. 1884.
    Euphrosyne ambrosiaefolia A. Gray, Pl. Wright. *1*:102. 1852.
    Cyclachaena ambrosiaefolia (A. Gray) Benth. and Hook., Ind. Kew. *1*:678. 1895.

Much branched annual, stems 3-8 dm. high, terete velutinous with both upwardly appressed and hispid hairs, or only appressed hairs; leaves alternate, ovate in outline, bipinnatifid with confluent segments, ultimate segments obtuse or acute and toothed, pubescent on both surfaces, sometimes hispid on the main veins, 5-6 cm. long; heads numerous, usually short peduncled in axillary spikes or panicles and terminal naked panicles; involucre hemispheric, 4-5 mm. broad, 2-2.5 mm. high; phyllaries 5, obovate to oblanceolate, sparingly hispid on the backs; paleae of the staminate flowers linear-spatulate; those of the pistillate flowers cuneate-obovate, obtuse to truncate, the apex entire or slightly erose; staminate flowers numerous, corolla about 1.5 mm. long, style about two-thirds as long as the stamens, stigma capitate, short penicillate; pistillate flowers 6-8 in each head, corolla vestigial or absent; achenes corky and ridged when immature, usually smooth and black at maturity, 1.2-1.5 mm. long. Figures 96-101.

Type: West Texas to El Paso, New Mexico, May-October 1849, *Wright 310* (G). Isotype: (US).

Distribution: New Mexico to Arizona, south to Sonora and Nuevo Leon in Mexico, east to western Texas.

Representative specimens.—UNITED STATES. ARIZONA. *Cochise Co.:* Outwash soil, 5500 ft., Paridise, Chiricahua Mts., 16 September 1907, *Blumer 1702* (F, G, US). *Greenlee Co.:* Blue River, Clifton, 10 September 1902, *Davidson 715* (G). *Pima Co.:* 12 mi. S. of Tucson, 13 September 1903, *Thornber 125* (NY, UC, US). *Pinal Co.:* Sacaton, 1864, *Harrison* (US). *Santa Cruz Co.:* Near Ft. Huachuca, 1883, *Lemmon 303* (G). NEW MEXICO. *Dona Ana Co.:* On mesa west of Organ Mts., 4000 ft., 30 September 1907, *Wooton & Standley* (US). *Grant Co.:* Mangas Springs, 24 September 1903, 4770 ft., *Metcalf 782* (G, UC, US). *Hidalgo Co.:* Desert pavement near Arrayo 10 mi. S. W. of Lordsburg, 24 September 1944, *Barkley 14788* (TEX, UC). *Sierra Co.:* Trujillo Creek, gravelly hills, 14 September 1904, *Metcalf 1344* (G, NY, UC, US). *Luna Co.:* Byer's Spring, 27 August 1895, *Mulford 1066* (MOB, US). TEXAS. *Brewster Co.:* Baldy flats, Glass Mt., 2 July 1940, *Warnock W221* (MOB, TEX, UC). *El Paso Co.:* El Paso, 10 September 1883, *Jones 4188* (F, G, NY, US). *Hudspeth Co.:* Mixed gypseous-calcareous soil near upper end of Ammonite Canyon, Malone Mts., 11 October 1944, *Waterfall 5810* (G, NY). *Jeff Davis Co.:* Jeff Davis Mts., 5 September 1918, *Young* (TEX, UC). *Pecos Co.:* Canyon of Palo Blanco Creek above fork, Tierra Viega Mts., 1 July 1941, Hinckley (TEX). *Presideo Co.:* Redford, along dry creek beds, 7 August 1909, *Hanson 787* (G, US).

MEXICO. *Chihuahua.* 5 mi. S. E. from San Carlos, silty desert plains, 10 August 1940, *Johnston* & *Muller 84* (G); 40 mi. S. of Villa Ahumada, grassland wash, 18 August 1957, *Jackson 2729* (KANU); mountain slopes near Cuidad Juarez, 1911, *Sterns* (NY); hills and plains near Chihuahua, October 1885, *Pringle 279* (F, G, NY, US). *Coahuila.* San Lorenzo de Laguna and vicinity, 22-27 leagues S. W. of Parras, August 1880, *Palmer 573* (F, NY, US). *Durango.* 1896, *Palmer 482* (F, G, UC, US); hills about Tlahualilo, 1500 m., 27 August 1905, *Pittier 490* (US). *Sonora.* Mesa de los Carrerds, west of Colonia Marelos, 25-26 September 1941, *White 4544* (G). *Zacatecas.* Sierra Madres, 18 August 1897, *Jones 2408* (NY, US).

19. *Iva ambrosiaefolia* subsp. *lobata* (Rydb.) Jackson, comb. nov.
Cyclachaena lobata Rydb. N. Am. Fl. I. 33:10. 1922.

Much branched annual, stems 3-8 dm. high, terete, hispid below, hispid and glandular in the upper branches; leaves alternate, ovate in outline, bipinnatifid with confluent segments, ultimate segments obtuse or acute; inflorescence leaves sometimes only lobed; heads numerous, usually on rather long slender peduncles in a much branched, sparingly leafy inflorescence; involucre hemispheric, 4-5 mm. broad, 2-2.5 mm. high; phyllaries 5, ovate to oblanceolate, sparingly hispid on the backs; paleae subtending the staminate flowers linear-spatulate; those of the pistillate flowers cuneate-ovate, slightly erose at the apex; staminate flowers numerous, corollas about 1.5 mm. long, style about two-thirds as long as the stamens, stigma capitate, short-pencillate; pistillate flowers 6-8 in each head, corollas vestigial or absent; achenes corky and ridged when immature, usually smooth and black at maturity, 1.2-1.5 mm. long.

Type: MEXICO. *Nuevo Leon.* Monterrey, August 1911, *Alban* & *Arsene 208* (US); isotype: (MOB).

Distribution: Mexico, state of Coahuila, Nuevo Leon, San Luis Potosi, and Zacatecas.

Although the type specimen of ssp. *lobata* shows only pinnately lobed leaves, the leaves are usually indistinguishable from ssp. *ambrosiaefolia.* Subspecies *lobata* is better characterized by the hispid and glandular pubescence of the upper branches.

Representative specimens.—MEXICO. *Coahuila.* Parras, 8-28 June 1880, *Palmer 574* (US); rocky cliff cut 31 mi. S. W. of Monterrey, 1 December 1945, *Warnoch* & *Barkley 14736M* (F, G, TEX). *Nuevo Leon.* Monterrey, 19 August 1911, *Arsene 540* (NY); near

Monterrey, August 1911, *Abbon 208* (MOB). *San Luis Potosi.* Limestone cliffs, Estacion de Catorce, 25 July 1934, *Pennell 17576* (US); Vanegas, Saltillo road, alkaline plain, *Lundell 5740* (US); City of San Luis Potosi, 1877, *Schaffner 273* (G, NY). Zacatecas. Near Conception del Oro, 22 November 1902, *Palmer 384* (NY, US).

DOUBTFUL SPECIES

Iva connata Sessé & Moc. Pl. N. Hispan. ed. 1, 161. 1887-90.

This species was described from the Chilpanzingi Mountains of Mexico. A duplicate collection of the Sessé and Mocina collection is in the Chicago Natural History Museum. However, the only identified specimen of *Iva* in the collection was a sheet labeled *Iva fruticosa* which is *Iva cheriranthifolia.* The original collection of the *I. connata* may have been lost or later identified as another genus. A copy of the original description of the species is as follows:

Iva foliis, connatis, lanceolatis, serratis, caule herbaceo. Fl. Mex.

Caulis herbaceus, strictus, teres, glaber, striatus. Folia connata, lanceolata, serrata, glaberrima. Pedunculi terminalis capitati. Calyx communis, foliolis tribus, ovatus, membranaceis. Corollulae disci pleures: radii nullae. Semina quot calycis, folia obovata. Receptaculum nudum.

Habitat in Chilpanzingi Montibus. floret Julio. ♂.

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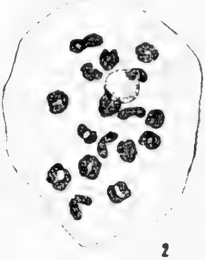
FIGURES 1 TO 10

FIGURES 1 to 10. Meiotic chromosomes of various species of *Iva*

FIG. 1. *I. acerosa* at diakinesis.
FIG. 2. *I. frutescens* at diakinesis.
FIG. 3. *I. asperifolia* at diakinesis.
FIG. 4. *I. angustifolia* at diakinesis.
FIG. 5. *I. dealbata* at prophase II.
FIG. 6. *I. microcephala* at telophase II.
FIG. 7. *I. texensis* at diakinesis.
FIG. 8. *I. ambrosiaefolia* at diakinesis.
FIG. 9. *I. xanthifolia* at prophase II.
FIG. 10. *I. annua* at diplotene.
All figures × 2000.

Figures 1-10

1



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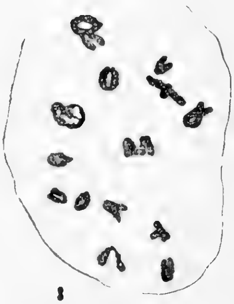

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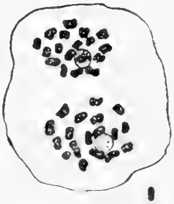

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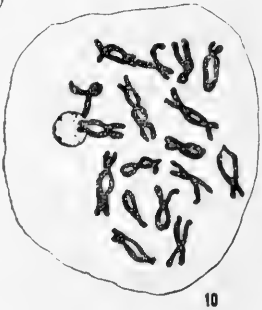

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FIGURE 11

FIG. 11. A phylogenetic interpretation of *Iva*.

FIGURE 11

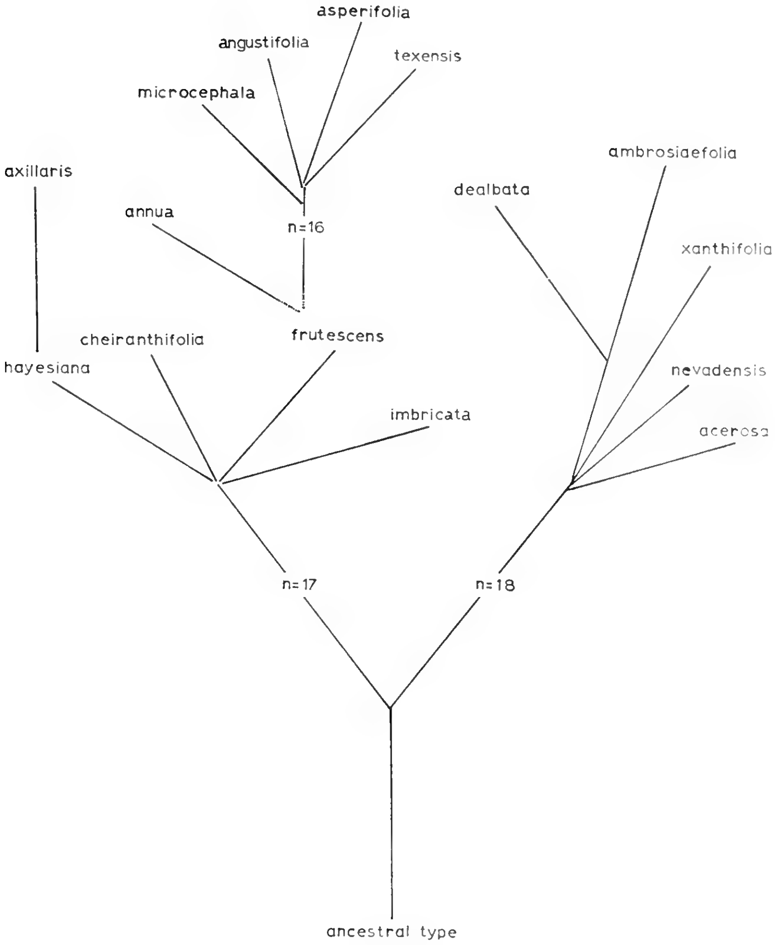


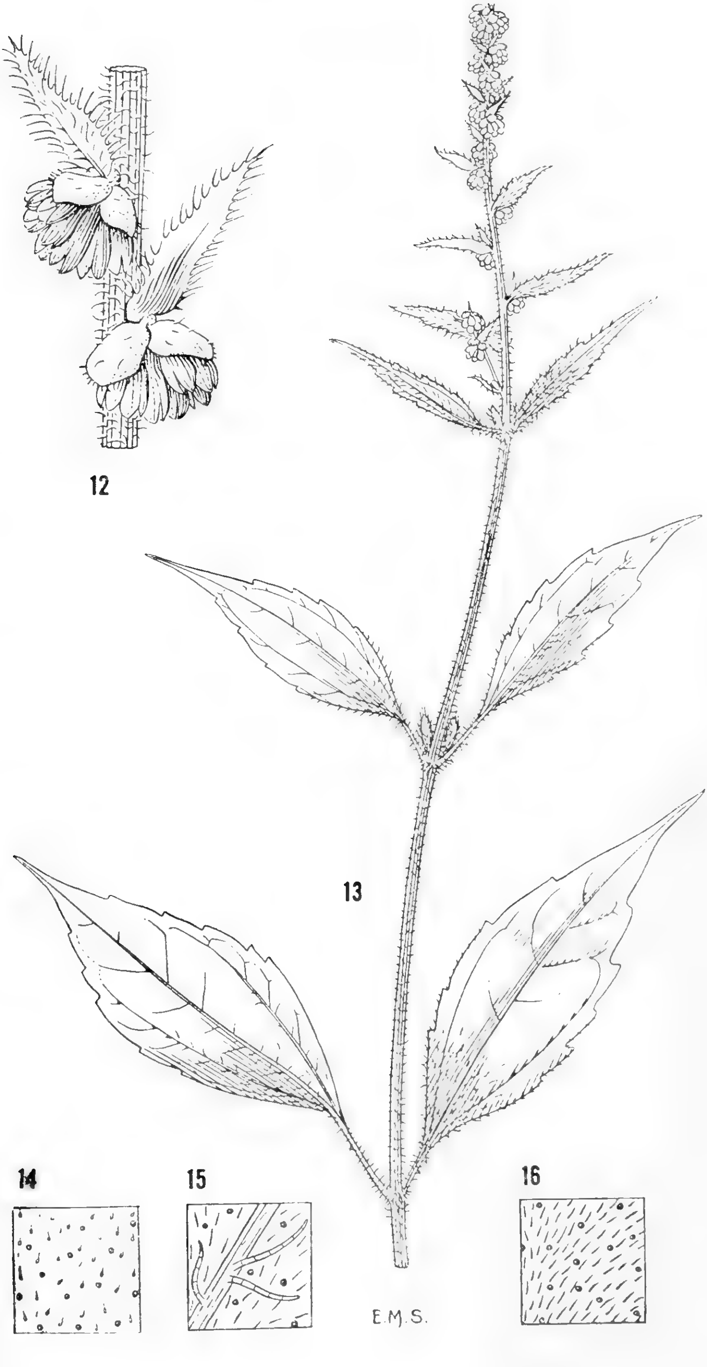
Fig. 11. A phylogenetic interpretation of IVA

FIGURES 12-16

FIGURES 12 to 16. Drawings from the type specimen of *Iva annua* L. by Margaret Stones

FIG. 12. Portion of inflorescence, × 6.
FIG. 13. Habit, × ½ natural size.
FIG. 14. Upper leaf surface, × 9.
FIG. 15. Lower leaf surface, × 9.
FIG. 16. Lower leaf surface near apex, × 9.

Figures 12-16

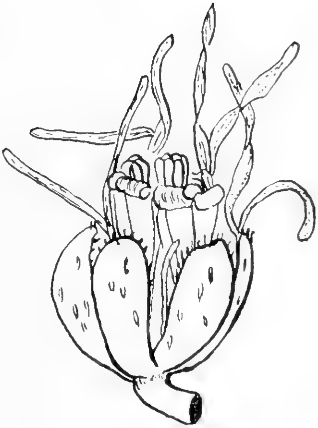


FIGURES 17-22

FIGURES 17 to 22, *Iva microcephala*

FIG. 17. Head, × 10.
FIG. 18. Median leaf, × 1.
FIG. 19. Pistillate flower, × 20.
FIG. 20. Palea of a staminate flower, × 20.
FIG. 21. Disc flower, × 20.
FIG. 22. Palea of a pistillate flower, × 20.

FIGURES 17-22



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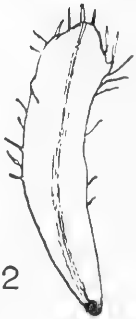


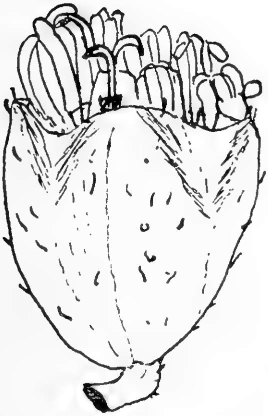
22

FIGURES 23-27

FIGURES 23 to 27. *Iva asperifolia*

FIG. 23. Head, × 10.
FIG. 24. Pistillate flower, × 25.
FIG. 25. Palea of a staminate flower, × 25.
FIG. 26. Staminate flowers, × 25.
FIG. 27. Median leaf, × 1.

FIGURES 23-27



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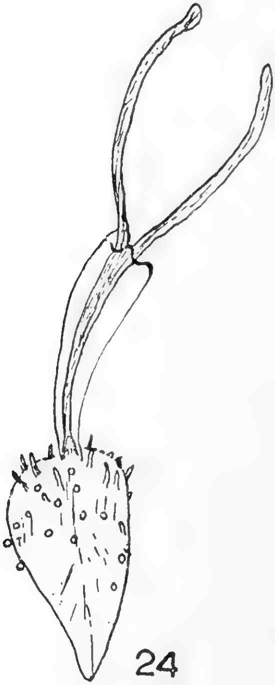

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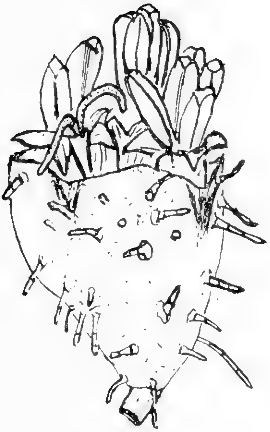
FIGURES 28-32

FIGURES 28 to 32. *Iva angustifolia*

FIG. 28. Head, × 10.
FIG. 29. Pistillate flower, × 25.
FIG. 30. Staminate flower, × 25.
FIG. 31. Palea of a staminate flower, × 25.
FIG. 32. Stem leaf, × 1.

Figures 28-32



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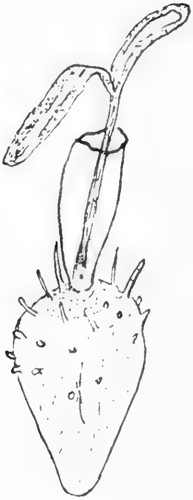

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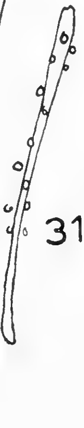

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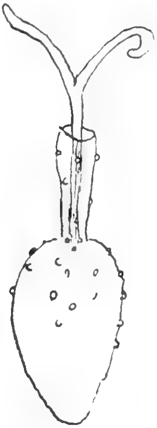
FIGURES 33-37

FIGURES 33 to 37. *Iva texensis*

FIG. 33. Involucre, × 15.
FIG. 34. Pistillate flower (young), × 20.
FIG. 35. Staminate flower, × 20.
FIG. 36. Palea of a staminate flower, × 20.
FIG. 37. Median leaf, × 1.

FIGURES 33-37

33



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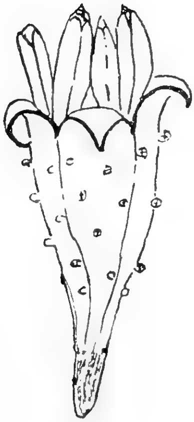

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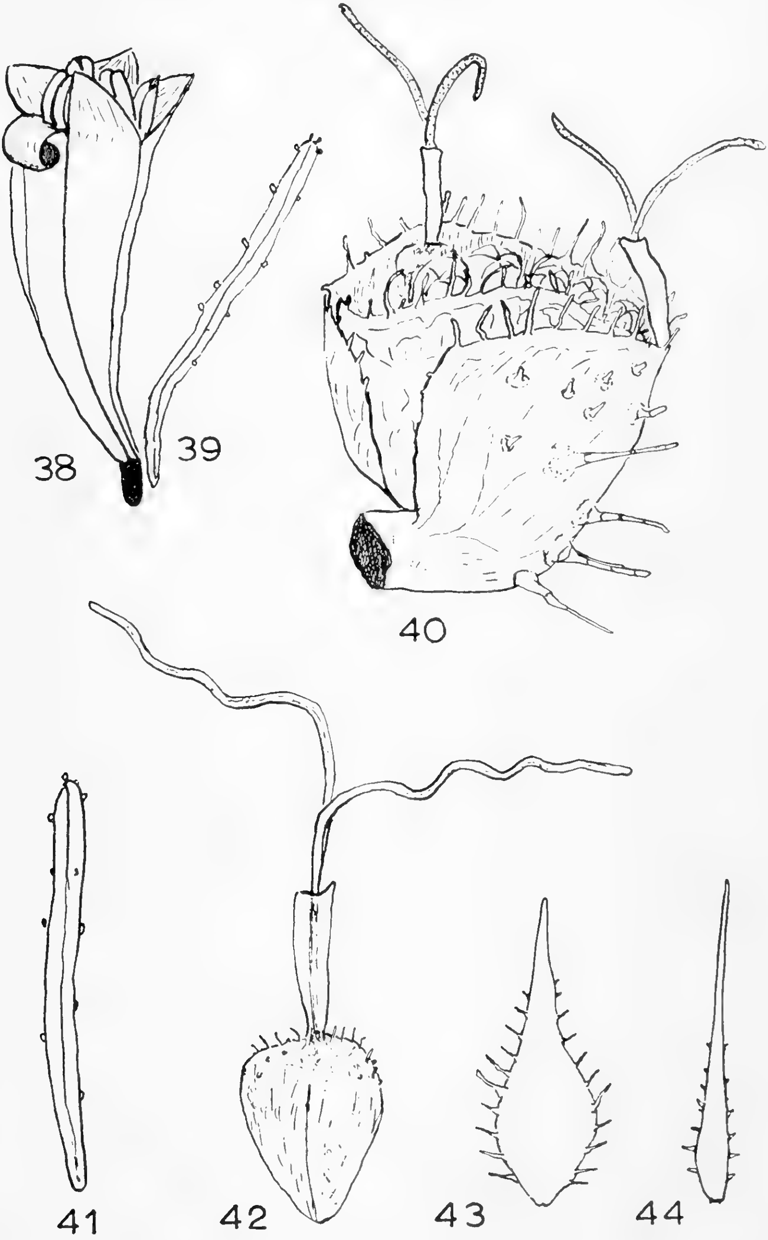
FIGURES 38-44

FIGURES 38 to 43. *Iva annua* var. *annua*

FIG. 38. Staminate flower, × 20.
FIG. 39. Palea of a staminate flower, × 20.
FIG. 40. Head, × 10.
FIG. 41. Palea of a pistillate flower, × 20.
FIG. 42. Pistillate flower, × 20.
FIG. 43. Inflorescence bract, × 3.
FIG. 44. Inflorescence bract of *Iva annua* var. *caudata,* × 3.

Figures 38-44

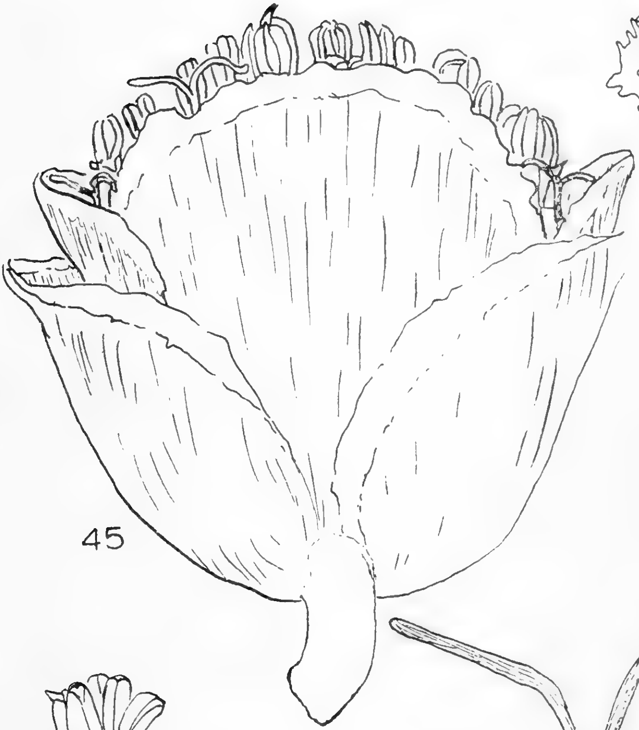


FIGURES 45-49

FIGURES 45 to 49. *Iva imbricata*

FIG. 45. Head, × 12.
FIG. 46. Palea of a staminate flower, × 10.
FIG. 47. Staminate flower, × 10.
FIG. 48. Palea of a pistillate flower, × 10.
FIG. 49. Pistillate flower, × 10.

Figures 45-49



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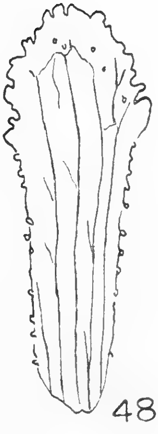

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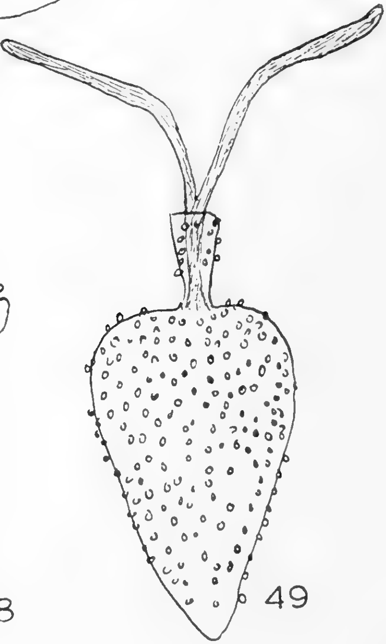

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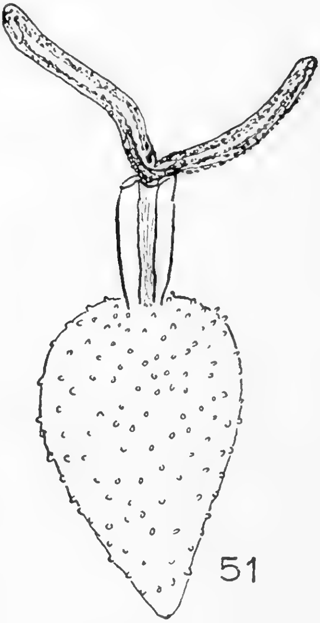
FIGURES 50-54

FIGURES 50 to 54. *Iva frutescens* ssp. *frutescens*

FIG. 50. Head, × 10.
FIG. 51. Pistillate flower, × 20.
FIG. 52. Staminate flower, × 20.
FIG. 53. Palea of a staminate flower, × 20.
FIG. 54. Palea of a pistillate flower, × 20.

FIGURES 50-54

50



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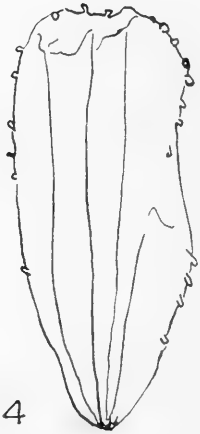

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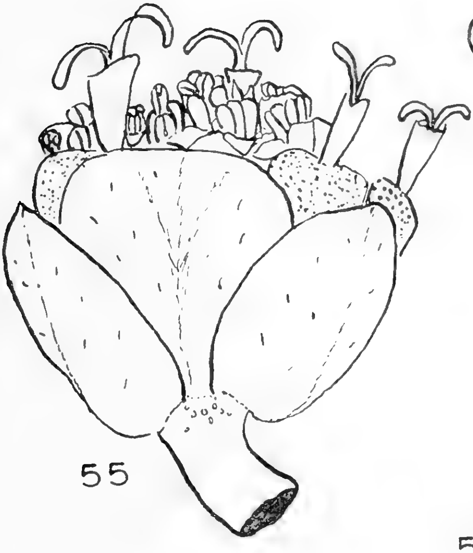
FIGURES 55-59

FIGURES 55 to 59. *Iva frutescens* ssp. *oraria*

FIG. 55. Head, × 10.
FIG. 56. Pistillate flower, × 20.
FIG. 57. Staminate flower, × 20.
FIG. 58. Palea of a staminate flower, × 20.
FIG. 59. Palea of a pistillate flower, × 20.

FIGURES 55-59



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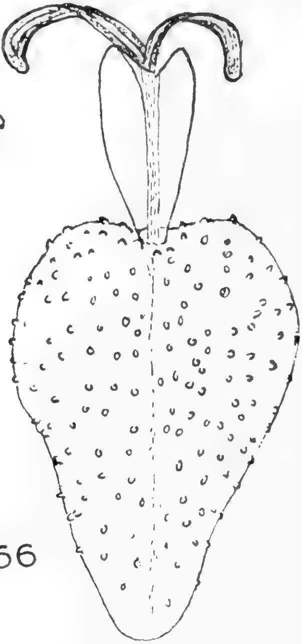

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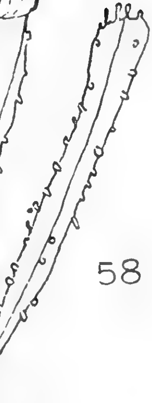

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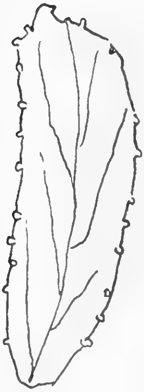

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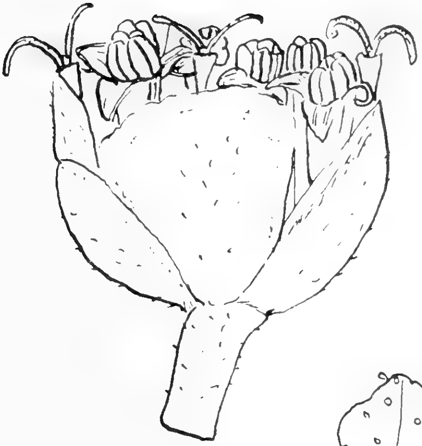
FIGURES 60-64

FIGURES 60 to 64. *Iva cheiranthifolia*

FIG. 60. Head, × 10.
FIG. 61. Pistillate flower, × 20.
FIG. 62. Palea of a staminate flower, × 20.
FIG. 63. Staminate flower, × 20.
FIG. 64. Palea of a pistillate flower, × 20.

FIGURES 60-64



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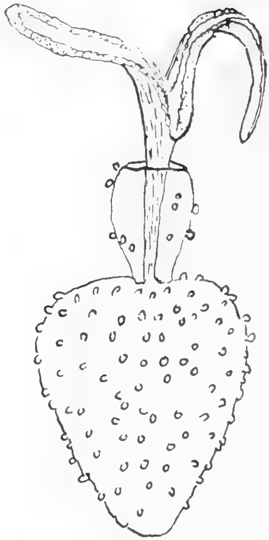

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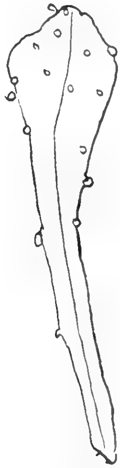

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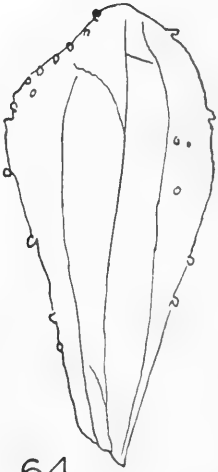


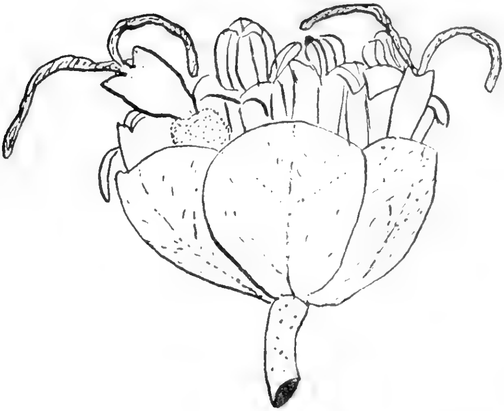
64

FIGURES 65-69

FIGURES 65 to 69. *Iva hayesiana*

FIG. 65. Head, × 10.
FIG. 66. Palea of a pistillate flower, × 20.
FIG. 67. Staminate flower, × 20.
FIG. 68. Palea of a staminate flower, × 20.
FIG. 69. Pistillate flower, × 20.

Figures 65-69



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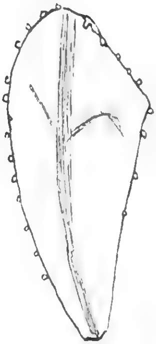

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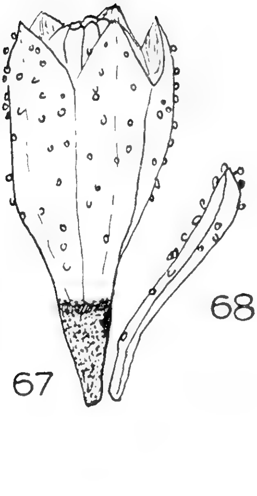

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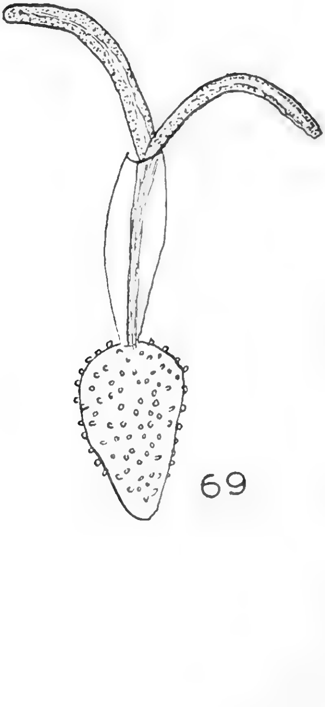

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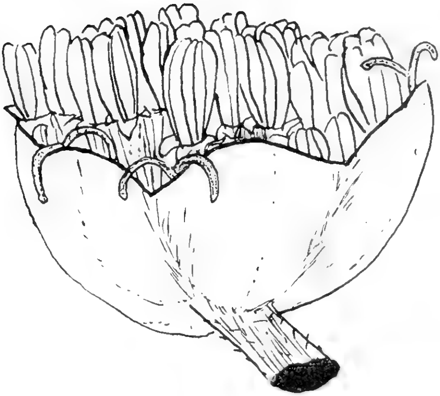
FIGURES 70-74

FIGURES 70 to 74. *Iva axillaris*

FIG. 70. Head, × 10.
FIG. 71. Pistillate flower, × 20.
FIG. 72. Staminate flower, × 20.
FIG. 73. Palea of a staminate flower, × 20.
FIG. 74. Palea of a pistillate flower, × 20.

Figures 70-74



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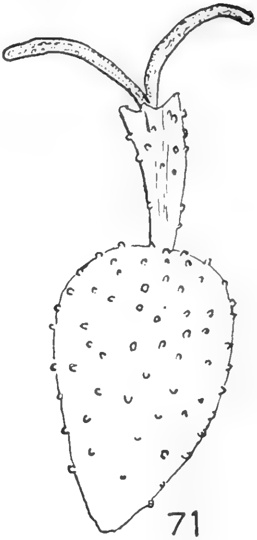

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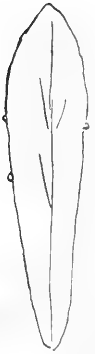

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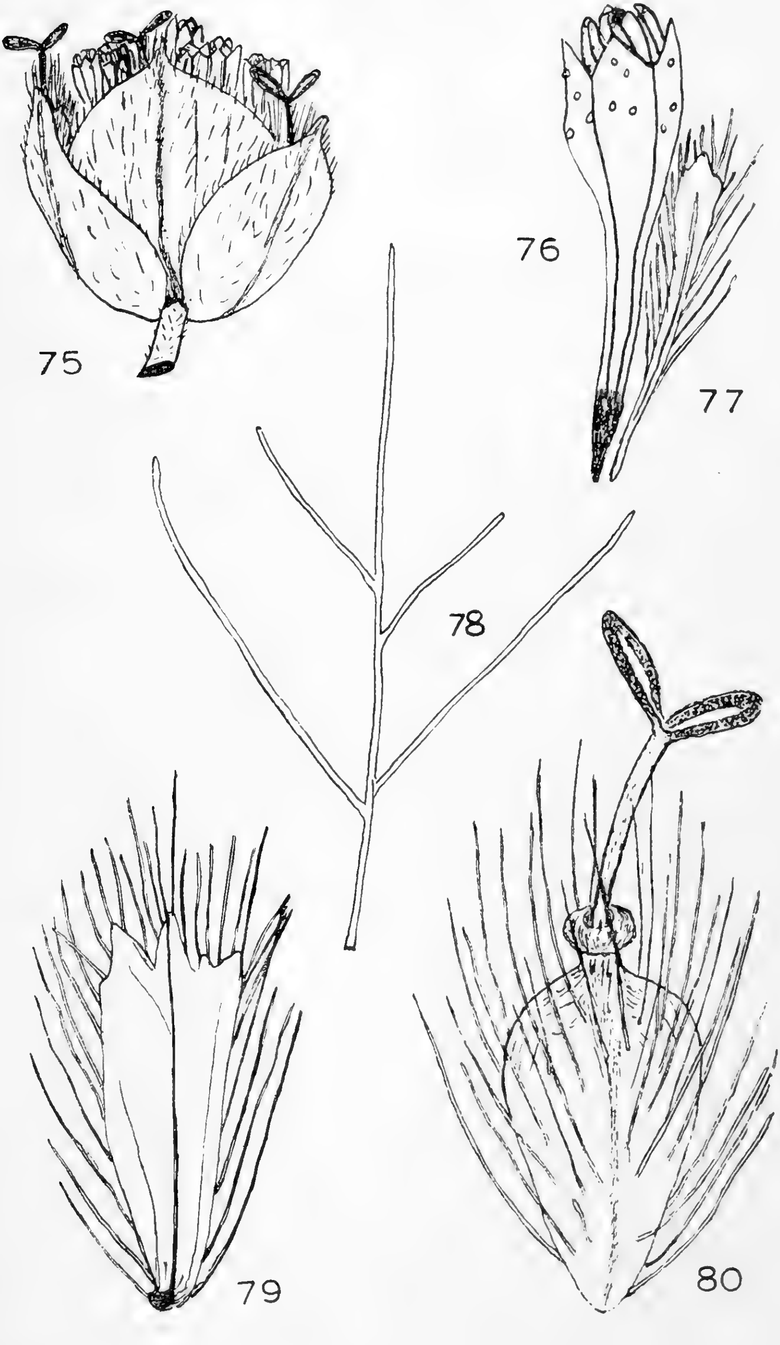
FIGURES 75-80

FIGURES 75 to 80. *Iva acerosa*

FIG. 75. Head, × 10.
FIG. 76. Staminate flower, × 20.
FIG. 77. Palea of a staminate flower, × 20.
FIG. 78. Median leaf, × 1.
FIG. 79. Palea of a pistillate flower, × 20.
FIG. 80. Pistillate flower, × 20.

FIGURES 75-80

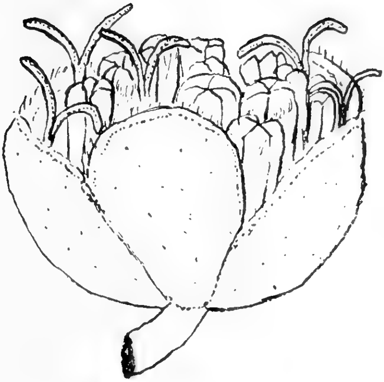


FIGURES 81-84

FIGURES 81 to 84. *Iva dealbata*

FIG. 81. Head, × 15.
FIG. 82. Median leaf, × 1.
FIG. 83. Pistillate flower, × 20.
FIG. 84. Staminate flower, × 20.

FIGURES 81-84



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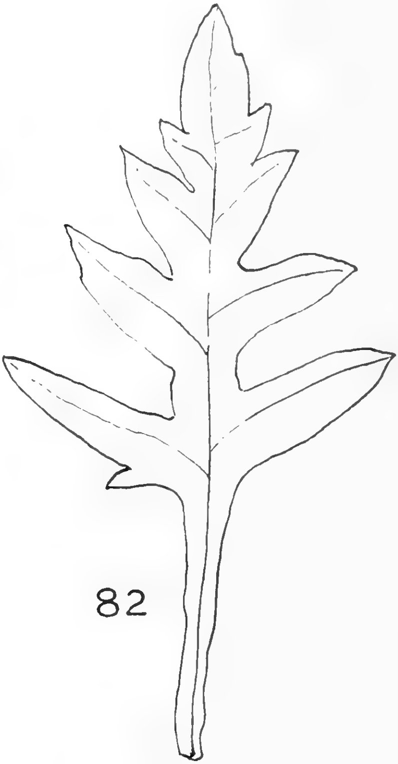

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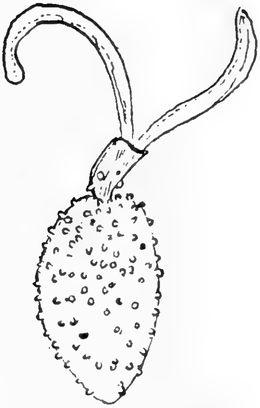

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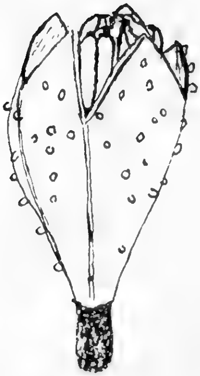

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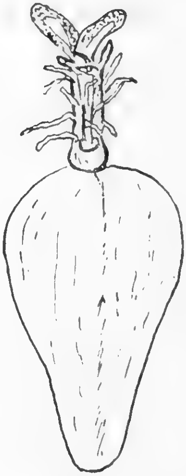
FIGURES 85-90

FIGURES 85 to 90. *Iva nevadensis*

FIG. 85. Head, × 15.
FIG. 86. Pistillate flower, × 20.
FIG. 87. Leaf, × 1.
FIG. 88. Staminate flower, × 20.
FIG. 89. Palea of a staminate flower × 20.
FIG. 90. Palea of a pistillate flower, × 20.

Figures 85-90

85



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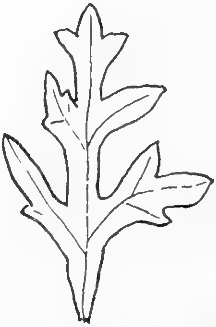

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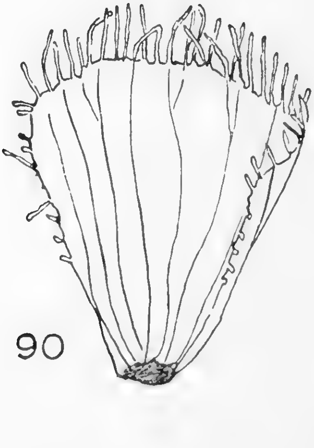

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FIGURES 91-95

FIGURES 91 to 95. *Iva xanthifolia*

FIG. 91. Head, × 15.
FIG. 92. Pistillate flower, × 20.
FIG. 93. Staminate flower, × 20.
FIG. 94. Palea of staminate flower, × 20.
FIG. 95. Palea of pistillate flower, × 20.

FIGURES 91-95

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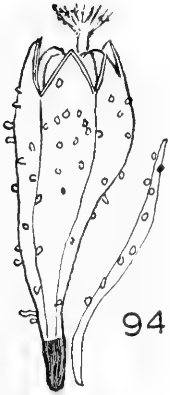

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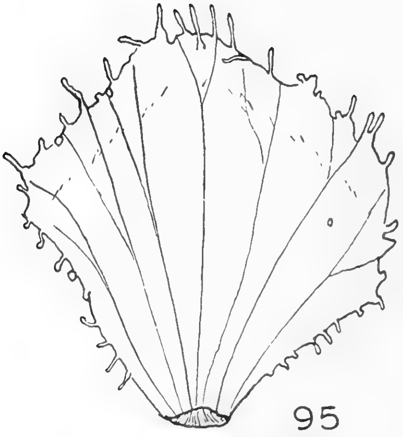

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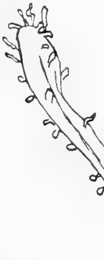
FIGURES 96-101

96



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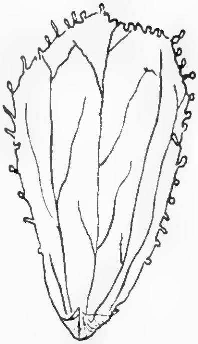

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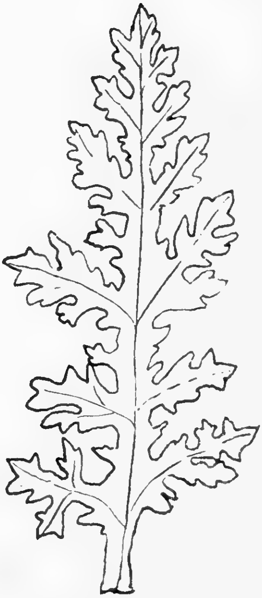

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FIGURES 96 to 101. *Iva ambrosiaefolia*

FIG. 96. Pistillate flower, × 20.
FIG. 97. Palea of a staminate flower, × 20.
FIG. 98. Staminate flower, × 20.
FIG. 99. Palea of a pistillate flower, × 20.
FIG. 100. Head, × 15.
FIG. 101. Upper stem leaf, × 1.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN
VOL. XLI] DECEMBER 23, 1960 [No. 8

Lung-Flukes of Snakes, Genera *Thamnophis* and *Coluber*, in Kansas

BY

PEGGY LOU STEWART

ABSTRACT: *Thamnophis sirtalis parietalis* Say and *Coluber constrictor flaviventris* Say were trapped and examined for lung-flukes on the University of Kansas Natural History Reservation, in Douglas County, in the months of June through November, 1958. These snakes were released at the points of capture after the flukes were removed. Also, examinations were made of preserved specimens of *T. sirtalis parietalis* Say, *T. radix haydeni* Kennicott, *T. sauritus proximus* Say, and *C. constrictor flaviventris* in the Museum of Natural History, the University of Kansas.

Crow (1913) reported *Natrix rhombifera, Ancistrodon* (*Agkistrodon*) *contortrix, A. mokassen* (= *A. c. mokeson*), *A. piscivorus*, and *Sistrurus miliarus* as hosts of lung-flukes in Kansas.

REVIEW OF THE TAXONOMY OF SOME TREMATODES IN REPTILES

Members of the order Digenea von Beneden are characterized by having the mouth opening within the oral sucker and an endoparasitic life in vertebrates. The members of the suborder Prosostomata Odhner, characterized primarily by having a subterminal mouth, are the only representatives of the Digenea that are parasitic in reptiles.

Yamaguti (1958) reviewed 29 families in Prosostomata, of which one, the Plagiorchiidae (Luhe, 1900) Ward (1917), comprises flukes having the distinctive character of tandem, diagonal, or symmetrical testes in the posterior half of the body.

Pratt (1902) defined the subfamily Reniferinae, in the family Plagiorchiidae. Pratt assigned to the Reniferinae those genera having the genital pore lateral to a point midway between the suckers: *Styphlodora* Looss (1899), *Astiotrema* Looss (1900), *Renifer* Pratt (1902), *Ochetosoma* Braun (1901), and Oistosomum Odhner (1902). Baer (1924) raised the Reniferinae to family level, Reniferidae.

Talbot (1934) included the following seven genera in the Reniferinae: *Macrodera* Looss (1899), *Renifer, Lechriorchis* Stafford (1905), *Zeugorchis* Stafford (1905) *Pneumatophilus* Odhner (1910), *Dasymetra* Nicoll (1911), and *Caudorchis* Talbot (1933).

Mehra (1937) placed in the subfamily Reniferinae sixteen genera, including *Macrodera, Renifer, Lechriorchis, Zeugorchis, Pneumatophilus, Natriodera* Mehra (1937), and *Pseudorenifer* Price (1936), especially pertinent to my discussion. He made use of the miracidia, sporocysts, and cercariae in assigning the mentioned genera to one subfamily. Adults of species in the Reniferinae, as recognized by Mehra, develop from xiphidiocercariae.

Byrd and Denton (1938) rediagnosed the subfamily Reniferinae and considered the following eight genera as members of the subfamily: *Renifer, Lechriorchis, Zeugorchis, Pneumatophilus, Dasymetra, Natriodera, Neorenifer* Byrd and Denton (1938), and *Paralechriorchis* Byrd and Denton (1938).

The genera *Styphlodora, Astiotrema, Ochetosoma,* and *Oistosomum* were excluded from the Reniferinae by Byrd and Denton, who agreed with Talbot (1934) that the positions of the genital pore and cirrus pouch of these genera exclude them from the subfamily as it was defined by Baer (1924).

Byrd and Denton (1938) opined that the subfamily Reniferinae should include genera having the genital pore in a position lateral to the digestive ceca or the pharynx. One genus, *Renifer,* including *R. ellipticus* Pratt (1902), is limited by these authors to those species having the genital pore lateral to the bifurcated ceca. *Renifer elongatus* Pratt (1903), *Renifer kansensis* Crow (1913), and *Renifer aniarum* Leidy (1891) are excluded because the genital pore is lateral to the oral sucker and pharynx.

Price (1936) concluded, after examining and redescribing Stafford's specimens in the genus *Zeugorchis* Stafford (1905) and in *Lechriorchis* Stafford (1905), that *Caudorchis* Talbot (1933) is synonymous with *Zeugorchis.* Price further considered *Zeugorchis bosci* Cobbold (1859), *Z. syntomentera* Sumwalt (1926), and *Z. megametricus* Talbot (1934) not to be congeneric with the type species *Z. aequatus* Stafford (1905). *Z. bosci* has the genital pore in a comparable position and ceca of approximately the same length as those members of the genus *Dasymetra* Nicoll (1911). Similar variables, such as genital pore posterior to or to one side of the bifurcation of ceca, are found in the other three species. Price (1935) established a new genus, *Pseudorenifer,* for *megametricus, ancistrodontis,* and *syntomentera,* whose anatomical features do not agree with those of *Z. aequatus*. *Pseudorenifer megametricus* Talbot (1934) was designated as the type species of the new genus.

According to Byrd and Denton (1938), *Zeugorchis* is characterized by the position of the genital pore, which is immediately posterior to the bifurcation of the ceca; and by the position of the testes, which are situated in the posterior fourth of the body. Since Price designated *megametricus* as the type species of the genus *Pseudorenifer*, in which the genital pore is lateral to the bifurcation of the ceca, Byrd and Denton consider the genera *Pseudorenifer* and *Renifer* to be synonymous.

For two groups of species that could not be placed in any named genus, Byrd and Denton (1938) proposed two new genera: *Paralechriorchis* comprising those species having the genital pore confined to the area between the acetabulum and the bifurcation of the ceca, and *Neorenifer* comprising those species having the genital pore at or near the margin of the body and in the region of the oral sucker and pharynx. The species *Renifer elongatus* Pratt, *Renifer kansensis* Crow and *Renifer aniarum* Leidy, among others, were assigned to the new genus *Neorenifer*.

DESCRIPTION OF NEW SPECIES

FAMILY RENIFERIDAE BAER, 1924

SUBFAMILY RENIFERINAE Pratt, 1902

Genus *Zeugorchis* Stafford, 1905

Zeugorchis megacystis, new species

(Pl. 1, Pl. 2)

Holotype.—No. 39104 U. S. National Museum, host *Thamnophis sirtalis parietalis* Say 5¾ mi. N. E. Lawrence, Douglas Co., Kansas; obtained on June 10, 1958, by Peggy Lou Stewart.

Paratypes.—No. 39106 (four individuals), U. S. National Museum, host species and locality of capture same as for holotype; obtained on June 10, July 7, 19, and 30, all in 1958.

Diagnosis.—Body attenuated anteriorly, length 2.5 mm., width 0.66 mm. (relaxed living example); entire cuticula randomly spinose; oral sucker subterminal; acetabulum immediately anterior to middle of body, larger than oral sucker; prepharynx shorter than pharynx; esophagus longer than combined length of prepharynx and pharynx; intestinal ceca extending slightly beyond posterior extremity of acetabulum; genital pore median to right cecum, posterior to anterior extremity of acetabulum; cirrus pouch narrowly ovoid, larger posteriorly; testes oval, in posterior third of body; ovary oval, overlapping posterior margin of acetabulum; uterus convoluted; excretory bladder ventral to uterus; vitellaria lateral, extending more anteriorly than posteriorly from middle of body; ova numerous, yellow-brown, 0.02 to 0.05 mm. by 0.01 to 0.02 mm; parasitic in digestive and respiratory tracts of *Thamnophis sirtalis parietalis, T. radix haydeni,* and *T. sauritus proximus.*

Measurements of holotype and variations in corresponding measurements of paratypes.*

	Length	Width	Thickness
Body	2.63±0.35(2.54)	0.72±0.06(0.66)	0.22±0.02
Oral sucker	0.35±0.01(0.45)	0.30±0.02(0.35)	0.21±0.02
Acetabulum	0.41±0.07(0.46)	0.46±0.01(0.48)	0.09±0.01
Prepharynx and pharynx	0.06±0.01(0.14)	0.15±0.01(0.14)	0.11±0.02
Esophagus	0.16±0.02(0.22)	0.12±0.01(0.06)	0.10±0.01
Ceca	0.79±0.03(0.72)	0.06±0.02(0.05)	0.02±0.01
Genital pore	....	0.01±0.01(0.01)	0.02±0.01
Cirrus pouch	0.34±0.01(0.40)	0.12±0.01(0.16)	0.06±0.01
Testes	0.02±0.02(0.21)	0.09±0.03(0.05)	0.16±0.03
Sperm duct	1.34±0.05(....)	0.04±0.01(....)	0.03±0.01
Ovary	0.09±0.01(0.09)	0.05±0.02(0.05)	0.10±0.02
Uterus	....	0.25±0.16(0.42)	0.08±0.04
Excretory bladder	0.27±0.01(0.28)	....	....
Excretory tube	....	0.02±0.02(....)	0.02±0.02
Vitelline span	0.87±0.03(0.93)	....	....

* Measurements of holotype are in parentheses. Dimensions are in millimeters.

Comparisons.—Among named kinds of *Zeugorchis, Z. megacystis* most closely resembles *Z. eurinus* Talbot (1933). From *Z. eurinus, Z. megacystis* differs as follows: length of body averaging approximately 2.5 *versus* 2.4 mm.; vitellaria in larger part anterior instead of posterior to middle of body; oral sucker smaller than, instead of approximately same size as, acetabulum. From *Zeugorchis syntomenteroides* Parker (1941), *Z. megacystis* differs as follows: body attenuate anteriorly instead of broad; length of body averaging approximately 2.5 *versus* 2.0 mm.; genital pore on same vertical plane as anterior margin of acetabulum instead of farther anteriorly immediately posterior to bifurcation of ceca; testes in posterior third rather than middle third of body; ovary oval instead of spherical. From *Zeugorchis aequatus* Stafford (1905), the type species of the genus, *Z. megacystis* differs as follows: body attenuate anteriorly instead of broad; length of body averaging approximately 2.5 *versus* 1.0 mm.; acetabulum larger than oral sucker instead of smaller than oral sucker; ceca extending to posterior edge of acetabulum instead of extending immediately anterior to testes; genital pore posterior to anterior extremity of acetabulum instead of directly posterior to bifurcation of ceca; testes in posterior third instead of posterior fifth of body; ovary overlapping posterior margin of, instead of posterior to, acetabulum; vitellaria extending more anteriorly than posteriorly instead of equally anteriorly and posteriorly from middle of body.

Genus *Neorenifer* Byrd and Denton, 1938

Neorenifer lateriporus, new species

(Pl. 1, Pl. 2)

Holotype.—No. 39105 U. S. National Museum, host *Coluber constrictor flaviventris* Say; 5¾ mi. N. E. Lawrence, Douglas Co., Kansas; obtained on September 8, 1958, by Peggy Lou Stewart.

Paratypes.—No. 39107 (three individuals) U. S. National Museum, host species and locality of capture same as for holotype; obtained on June 9, July 25, and August 12, all in 1958.

Diagnosis.—Body slightly attenuated anteriorly and posteriorly; length 5.24 mm., width 0.83 mm. (relaxed living example); cuticula without spines; oral sucker subterminal; acetabulum immediately anterior to middle of body, larger than oral sucker; prepharynx absent; pharynx longer than esophagus, intestinal ceca extending slightly posterior to anterior extremity of testes; genital pore lateral

Measurements of holotype and variations in corresponding measurements of paratypes.**

	Length	Width	Thickness
Body	5.84 ± 0.16(5.24)	1.43 ± 0.27(0.83)	0.30 ± 0.02
Oral sucker	0.36 ± 0.04(0.27)	0.44 ± 0.18(0.31)	0.22 ± 0.17
Acetabulum	0.42 ± 0.02(0.41)	0.48 ± 0.05(0.43)	0.10 ± 0.04
Pharynx	0.25 ± 0.03(0.23)	0.41 ± 0.12(0.25)	0.34 ± 0.10
Esophagus	0.27 ± 0.09(0.22)	0.14 ± 0.12(0.06)	0.14 ± 0.10
Ceca	2.04 ± 0.16(1.92)	0.08 ± 0.04(0.08)	0.04 ± 0.03
Genital pore	0.02 ± 0.01(. . . .)	0.14 ± 0.01(0.13)	0.14 ± 0.01
Cirrus pouch	1.23 ± 0.01(0.88)	0.16 ± 0.01(0.14)	0.08 ± 0.01
Testes	0.53 ± 0.07(0.46)	0.32 ± 0.11(0.25)	0.20 ± 0.09
Ovary	0.39 ± 0.04(0.16)	0.24 ± 0.17(0.15)	0.17 ± 0.08
Uterus	0.71 ± 0.65(. . . .)	0.21 ± 0.06(0.59)	. . . .
Excretory bladder	1.48 ± 0.05(1.32)	. . . .	. . . .
Excretory tube	. . . .	0.08 ± 0.02(. . . .)	0.08 ± 0.02
Vitelline span	1.51 ± 0.06(1.32)	. . . .	. . . .

** Measurements of holotype are in parentheses. Dimensions are in millimeters.

on right side of body; cirrus pouch narrowly ovoid, larger posteriorly than elsewhere, ending anterior to acetabulum; ovary lobed; testes oval, immediately posterior to middle of body; uterus convoluted; excretory bladder ventral to uterus; vitellaria lateral, extending more anteriorly than posteriorly from middle of body; shell gland not distinct; ova numerous, brown, 0.02 to 0.05 by 0.02 mm.; parasitic in digestive and respiratory tracts of *Coluber constrictor flaviventris.*

Comparisons.—Of the other 13 species in the genus *Neorenifer, N. orula* Talbot (1934), the type species of the genus, seems to be the closest relative of *N. lateriporus.* From *N. orula, N. lateriporus* differs as follows: genital pore on right instead of left margin of body; body less attenuated posteriorly; length averaging 5.8 *versus* 2.0 mm.; ceca overlapping anterior margin of testes instead of terminating posterior to testes; testes in middle, not posterior, third of body; ovary lobed instead of spherical; host, *Coluber constrictor flaviventris* instead of *Natrix sipedon.* The absence, instead of presence, of cuticular spines in *N. lateriporus* is the principal difference between it and *N. sauromates* Poirier (1885), *N. zschokkei* Volz (1899), *N. elongatus* Pratt (1903), *N. formosum* Nicoll (1911), *N. validus* Nicoll (1911), *N. kansensis* Crow (1913), *N. wardi* Byrd (1936), and *N. heterodontis* Byrd and Denton (1938). A difference from *N. acetabularis* Crow (1913) and *N. aniarum* Leidy (1891) is the absence instead of presence of a dichotomous pattern of the vitelline follicles in an anteroposterior plane. Differences from *N. serpentis* Schmidt and Hubbard (1940) are: body fusiform instead of ovoid; length averaging 5.8 instead of 2.8 mm.; shell gland indistinct instead of distinct; uterus convoluted instead of non-convoluted; host, *Coluber constrictor flaviventris* instead of *Agkistrodon piscivorus.* Differences from *N. septicus* MacCallum (1921) are: longer (5.8 *versus* 3.3 mm.); ceca extending beyond level of ovary instead of to level of ovary; uterus convoluted instead of non-convoluted; excretory pore opening at posterior extremity, rather than anterior to posterior end, of body.

INFECTION AND NATURAL HISTORY OF SNAKES EXAMINED

Thamnophis.—Ninety-eight living *T. sirtalis parietalis* on the reservation (June through November, 1958) and 326 preserved *Thamnophis sirtalis parietalis, T. radix haydeni, T. sauritus proximus* in the museum collection (1899 through 1957) were examined for fluke infections. Thirty-three *Zeugorchis megacystis* were found in a total of 17 of the snakes on the reservation, and 26 in a total of 6 of the snakes in the museum. Five was the largest number of flukes found in a single live snake, and 8 was the largest number found in a preserved snake.

Adult individuals of *Zeugorchis megacystis* were taken from the digestive tracts of the snakes on the reservation, and from the digestive and respiratory tracts of the snakes in the museum.

The majority of lung-flukes that were obtained from living and preserved snakes came from specimens collected in June and July.

Of the living snakes, 4 of 39 males and 13 of 59 females were infected by *Zeugorchis megacystis.*

Lengths and weights of infected and noninfected snakes were measured on the reservation. Because of the small number of infected snakes, the size-differences between individual snakes could not certainly be attributed to the effects of parasitism.

More than one hundred double traps were distributed in various habitats (including forest and prairie) on the reservation, in May. In the autumn, all of the traps were moved to rock ledges. None of the snakes trapped on the ledges was infected.

In the museum collection, trematodes were found in two snakes from Douglas County and in one each from Anderson, Stafford, Wallace and Morton counties. The specimens studied represented 55 counties, with the majority having been collected in eastern, south-central, and northwestern Kansas.

Coluber.—One hundred and twenty-three *C. constrictor flaviventris* were examined on the reservation and 294 in the museum collection. Seven of the live snakes contained a total of 13 *Neorenifer lateriporus*, whereas 19 preserved snakes were infected by a total of 122 lung-flukes. The largest number of flukes found in a single live snake was 3, in a preserved snake, 41.

The regions of infection of *N. lateriporus* in living and preserved *C. constrictor flaviventris* were the same as those of *Z. megacystis* in *Thamnophis.*

Major infections occurred in June and July in living snakes, and in preserved snakes collected in June, July, and September.

Fifty-two male and 71 female snakes were examined on the reservation; 3 males and 4 females contained lung-flukes.

Variations in length and weight of *C. constrictor flaviventris* could not be attributed to parasitism by *N. lateriporus.*

Infected and noninfected *C. constrictor flaviventris* were trapped on most of the reservation area.

Among the 26 snakes captured in Douglas County, 4 contained

N. lateriporus. Eight additional counties yielded infected snakes: Gove, seven; Clark, two; and Anderson, Graham, Neosho, Stafford, Wyandotte, one each. The study included specimens from 44 counties, with collections having been made primarily in eastern, south-central, and northwestern Kansas.

ATTEMPTS TO DISCOVER THE LIFE CYCLES OF THE FLUKES

Samples of snake scats (fecal material) were examined for ova. Eleven scat samples from *Thamnophis* contained trematode ova. These ova were of the same dimensions as ova within the uteri of *Z. megacystis.* None of the scat samples obtained from *C. constrictor flaviventris* contained trematode ova.

Snails, *Helisoma trivolvis lentum* and *Physa hawni,* were collected once a week from June 19 through July 24, 1958. Daily, over a period of six weeks, snails of the two species were macerated and examined for sporocysts and rediae. None was found.

Water samples from culture dishes containing snails were examined for cercariae, twice daily, from June 19 through July 31, 1958. The samples were negative.

The frog, *Rana pipiens* Schreber, was the primary food source for the *T. sirtalis parietalis* and *C. constrictor flaviventris* trapped on the reservation. Approximately 50 *R. pipiens* were collected near the reservation from June 26 through July 31, 1958. The frogs were dissected and examined, but no metacercariae were found.

Possible intermediate hosts found in the digestive tracts of *Coluber* and *Thamnophis* were: earthworm, *Lumbricus* sp.; voles *(Microtus)*; toads, *Scaphiopus bombifrons* Cope, *Bufo terrestris* Bonaterre, and *Bufo woodhousei* Girard; frogs, *Acris gryllus* Le Conte, *Hyla versicolor* Le Conte, *Pseudacris nigrita* Le Conte, *Gastrophryne olivacea* Hallowell, and young *Rana catesbeiana* Shaw.

During dry weather, the frogs and toads inhabited the edges of the two reservation ponds; in wet weather they approached uniform dispersal throughout the reservation. Rainfall in the months of 1958 when collections were made was great enough to afford ample opportunity for the snakes to capture intermediate hosts of lungflukes at or near all of the trap sites (assuming toads or frogs act as hosts for *Z. megacystis* and *N. lateriporus*).

In snakes examined from the reservation, no parasites (of bodypart checked) were found, other than the two kinds described herein.

SUMMARY AND DISCUSSION

Zeugorchis megacystis is parasitic in the lungs and upper digestive tract of *Thamnophis sirtalis parietalis, T. radix haydeni,* and *T. sauritus proximus.*

Neorenifer lateriporus is parasitic in the lungs and upper digestive tract of *Coluber constrictor flaviventris.*

Although differences of size were found between infected and noninfected snakes, both in males and in females, several factors complicate interpretation of these data: The relatively small number of infected snakes, the limited period in which they were collected, and the effects of bearing young. It is uncertain that differences in length-weight ratios can be attributed to parasitism.

Flukes were found in the mouth and pharynx of snakes caught in spring and summer (but not in autumn) and in the lung region in autumn. Probably some, if not all, adult lung-flukes migrate to the lungs from the mouth and pharyngeal regions at the advent of the hibernation season of the snakes.

The geographical distribution of infected snakes in Kansas showed no significant difference from that of noninfected snakes.

The pond snails *Helisoma trivolvis* and *Physa hawni* were examined for intermediate stages of the life cycle of the two new species of flukes. None was found.

The amphibians considered most likely to serve as intermediate hosts for these flukes were those with geographic distributions corresponding most nearly with those of the host snakes. For this reason, I examined newly transformed and adult *Rana pipiens* from Douglas County for metacercariae, but found none.

Thanks go to the following for help: Miss Mary E. Larson, Dr. A. Byron Leonard, Dr. Kenneth B. Armitage, Dr. Henry S. Fitch, Dr. T. H. Eaton, and Dr. Frank B. Cross, of the University of Kansas, and to Dr. Raymond M. Cable, of Purdue University.

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PLATE 1

A. *Zeugorchis megacystis* n. sp. (dorsal view).
B. *Neorenifer lateriporus* n. sp. (dorsal view).

(a, b, c, d—represent cross section levels of Plate 2).

ac.	acetabulum
ce.	cecum
cp.	cirrus pouch
e.	esophagus
ep.	excretory pore (in a higher plane)
g.	genital pore
m.	metraterm
o.	ovary
os.	oral sucker
p.	pharnyx
t.	testis
u.	uterus
ub.	urinary bladder
v.	vitellaria

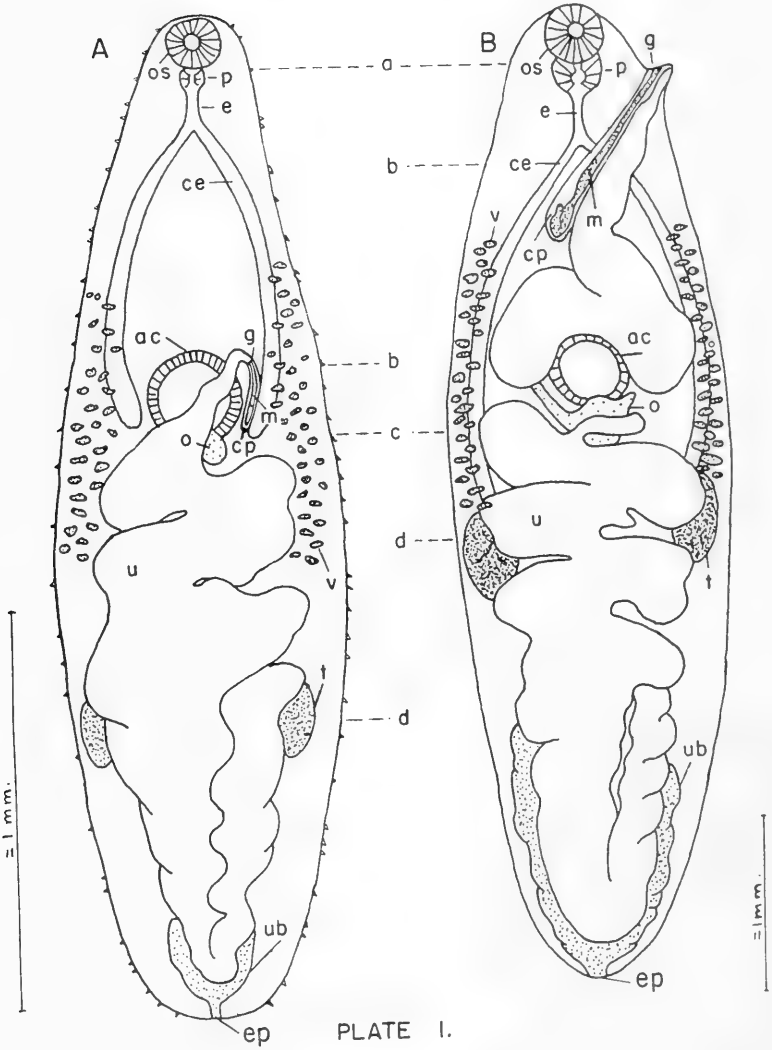

PLATE I.

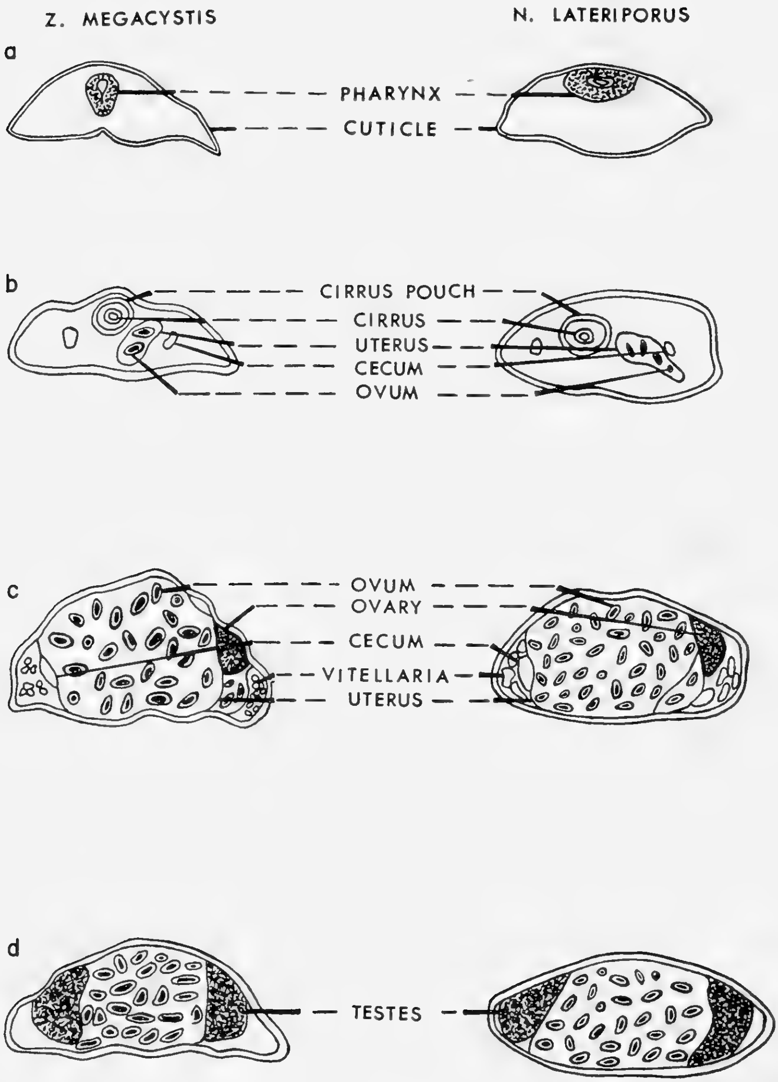

PLATE 2.

Cross section through *Zeugorchis megacystis* and *Neorenifer lateriporus*
a. Through pharnyx.
b. Through cirrus pouch.
c. Through ovary.
d. Through testes.

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A Survey of the Periotic Labyrinth in Some Representative Recent Reptiles

BY

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ABSTRACT: The periotic adnexa of the saccule and cochlear duct are described in some detail in fourteen reptilian families represented by a total of thirty species; brief accounts of parts of the otic labyrinth and otic capsule are included for those forms in which such descriptions seem appropriate. Modifications of the nomenclature applied to the reptilian periotic labyrinth are suggested, and certain new and hitherto-obscure periotic structures are described and named. Some suggestions concerning the evolution, the phylogenetic significance and the manner of function of the periotic labyrinth in reptiles are made and discussed.

TABLE OF CONTENTS

INTRODUCTION

The internal ear of reptiles has been subjected to considerable morphological study, and some reports of functional investigations appear in the literature; there has been, however, relatively little attention paid to the periotic labyrinth in these animals. Retzius (1884) in his classic work, summarizes the earlier literature and considers the parts of the otic labyrinth in detail, but he tends to neglect periotic structures both in figures and in text. Some attention has been accorded the system by de Burlet (1929, 1934), and brief references to it are found in papers devoted to the cranial or auditory anatomy of specific forms or groups. There has been, however, no comprehensive survey or interpretation of the periotic labyrinth in the Class Reptilia.

This investigation was undertaken in the hope of accomplishing at least three results: (1) to provide detailed descriptions of the periotic labyrinths of a number of representatives of each of the major taxonomic assemblages of living reptiles; (2) to augment the fund of information bearing upon the evolution of the vertebrate ear; and (3) to ascertain whether or not reptilian phylogeny is reflected by the structure of the inner ear in general, and the periotic labyrinth in particular. It was additionally hoped that the study might contribute something toward a better understanding of reptilian auditory function.

I am indebted to Dr. A. S. Romer for suggesting this investigation, and for his patience, suggestions and criticisms during its course. The late Dr. G. B. Wislocki, Dr. E. E. Williams and Mr. David Hamilton have also contributed to this effort by making available to me certain materials without which the study would have been less complete, and Miss Diane Allen has given valuable assistance in the preparation of the illustrations.

MATERIALS AND METHODS

This investigation was begun using serial sections of reptilian embryos from the Harvard Embryological Collection, Department of Anatomy, Harvard University. This material proved to be limited with respect to the selection of species available, and the number of late embryos representing each species; attention was, therefore, directed toward adult specimens, the findings from embryological material being utilized only in those forms for which adult representatives were not available. The forms used are listed below. Species designated "HEC" were studied from material in the Harvard collection; all others were represented by two or more serially-sectioned heads of adult animals.

- Order Chelonia
  - Family Chelydridae
    - *Chelydra serpentina*
  - Family Testudinidae
    - *Chrysemys marginata* (HEC)
    - *Chrysemys picta bellii*
    - *Pseudemys scripta elegans*
- Order Rhynchocephalia
  - Family Sphenodontidae
    - *Sphenodon punctatum* (HEC)
- Order Squamata
  - Suborder Lacertilia
    - Family Iguanidae
      - *Anolis carolinensis*
      - *Crotaphytus collaris baileyi*
      - *Sceloporus undulatus consobrinus*
      - *Uta stansburiana stansburiana*
      - *Phrynosoma cornutum*
      - *Phrynosoma douglassii brevirostre*
    - Family Eublepharidae
      - *Coleonyx variegatus*
    - Family Sphaerodactylidae
      - *Sphaerodactylus macrolepsis*
    - Family Gekkonidae
      - *Hemidactylus mabouia*
      - *Aristelliger praesignis*
    - Family Teiidae
      - *Cnemidophorus sexlineatus*
    - Family Scincidae
      - *Eumeces fasciatus*
      - *Eumeces obsoletus*
      - *Lygosoma weeksae* (HEC)
    - Family Lacertidae
      - *Lacerta muralis*
      - *Lacerta vivipara*
    - Family Anguidae
      - *Ophisaurus ventralis*
    - Family Varanidae
      - *Varanus sp.*

Suborder Ophidia
  Family Colubridae
    Carphophis amoena vermis
    Diadophis punctatus arnyi
    Lampropeltis calligaster calligaster
    Thamnophis ordinatus parietalis
    Thamnophis radix (HEC)
Order Crocodilia
  Family Crocodylidae
    Alligator sp.
    Caiman sp.

The primary method of approach in this investigation was the study of serially-sectioned material, supplemented by wax and/or graphic reconstructions. In the preparation of serial sections of the heads of adult animals, standard techniques for decalcification and sectioning did not prove to be satisfactory, since their application resulted either in excessive disruption of delicate parts of the otic and periotic labyrinths, or in loss of specimens due to lack of uniform decalcification and homogeneity in embedded tissue. A method was devised to overcome these difficulties, and a description of it will be published later.

In an attempt to clarify the relationship between the periotic and cerebrospinal fluid compartments, several specimens were subjected to radiographic study using the method of Young (1952). Several living anesthetized turtles and lizards were studied employing a modification of a technique originated and suggested orally by Dr. G. O. Proud, Department of Hearing and Speech, University of Kansas School of Medicine. In the latter method, an appropriate volume of cerebrospinal or periotic fluid was withdrawn, and replaced with an equal volume of 0.5 percent Evans Blue dye in reptilian Ringer's solution. After an appropriate interval, the animals were sacrificed and their otic regions dissected to determine the distribution of the dye.

The embryonic development of the periotic labyrinth was studied in several forms for which a number of developmental stages were available. Broadly speaking, the development of periotic spaces and definitive periotic connective tissues is similar to that in man, as described by Streeter (1918) and Bast and Anson (1949). One difference is worthy of note; in no case did late reptilian embryos (final day of incubation in *Eumeces fasciatus*) show complete differentiation of the periotic labyrinth. This contrasts sharply with the situation in man, in which differentiation is said to be "virtually complete—at the middle of fetal life" (Bast and Anson, 1949:114). Material which will permit more thorough study of the development of the labyrinth is now being collected.

STRUCTURE OF THE INTERNAL EAR IN REPTILES

The diverse origins of the early literature concerned with the vertebrate ear, plus differences in organization of its parts in the forms considered, have resulted in an extensive synonomy and some confusion in nomenclature. It is necessary, therefore, to define terms employed in this paper before describing the periotic systems of specific forms.

Bast and Anson (1949) follow suggestions of Streeter (1918) relative to nomenclature of the fluid compartments of the internal ear, and present a particularly lucid system of terminology applicable to the internal ear of man and most other mammals. Many of their terms may be applied accurately to the reptilian ear without modification; where possible, such application has been made. In other cases, either appropriate modifications of definitions have been made, or suitable terms applied.

In its basic organization, the internal ear in reptiles corresponds to the typical vertebrate pattern. Housed within a bony enclosure, the *otic capsule* (auditory capsule; osseus labyrinth), are intricate, membranous, fluid-filled channels and sacs which form two morphologically distinct systems. The innermost of these, the *otic labyrinth* (membranous labyrinth of some authors), is derived from the embryonic ectodermal otocyst and contains *otic fluid* (endolymph). The second system of channels, the *periotic labyrinth* (perilymphatic system), surrounds the otic labryrinth and contributes to its fixation within the otic capsule; it contains *periotic fluid* (perilymph).

The otic labyrinth (Fig. 1) may, arbitrarily, be divided into superior (vestibular; utricular) and inferior (saccular; auditory) divisions. The former consists of the *utricle* with its macula utriculi and macula neglecta, the anterior, posterior and lateral *otic semicircular ducts* and the three *otic ampullae*. A short *utriculosaccular duct* joins the utricle with the saccule. The inferior division consists of three major otic compartments, the intracranial *otic sac* (endolymphatic sac), the *saccule* with its *macula sacculi*, and the *cochlear duct* (lagena of some authors). The two compartments first named are united by the *otic duct* (endolymphatic duct); the

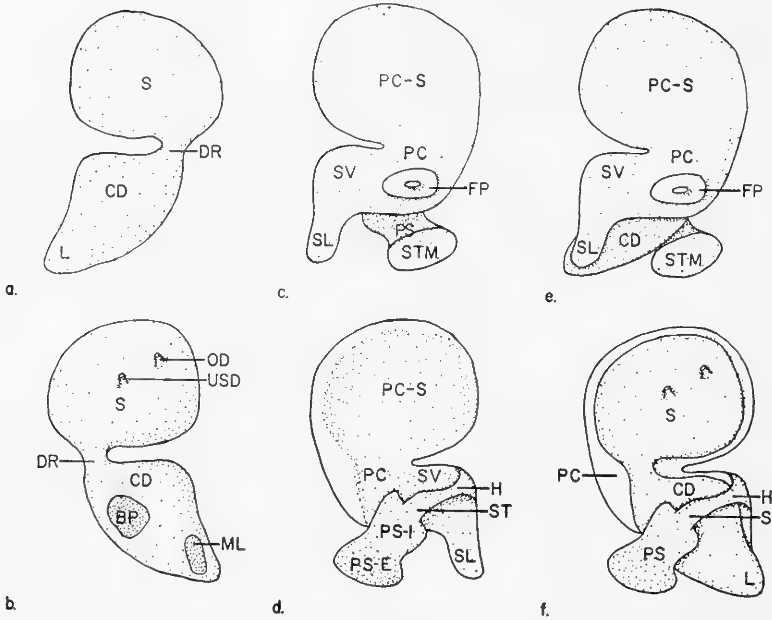

FIGURE 1. Diagram of intracapsular parts of the right otic labyrinth in a "typical" lizard; medial aspect.

saccule communicates, at or near its posterior margin, with the cochlear duct by way of the *ductus reuniens* (sacculo-cochlear canal).

The cochlear duct is uncoiled and roughly pyramidal in shape in most reptiles. An anteroventral projection of the cochlear duct is termed the *lagena* and carries an area of sensory epithelium, the *macula lagenae.* Proximal to the lagena, part of one wall (medial in most forms) of the cochlear duct is modified to form the *basilar papilla,* a receptor homologous to at least part of the sensory cells of the organ of Corti of mammals. The basilar papilla is seated upon the *basilar membrane,* a thin sheet of connective tissue supported by the *limbus* (Knorpelschenkel or cochlear cartilage). The latter term is here used, as defined by Shute and Bellairs (1953), to include the presumed homologs of both the limbus and spiral ligament of mammals. The limbus projects, in some forms, into the cochlear duct to form a *limbic lip* (Shute and Bellairs, *ibid.*) and may support a *tectorial membrane.* The opposite wall of the cochlear duct is thin and is designated *vestibular membrane* (tegmentum vasculosum).

The periotic labyrinth develops, and is situated in the adult, between the epithelium of the intracapsular parts of the otic labyrinth and the otic capsule; one part of the periotic labyrinth, as noted below, extends outside of the otic capsule. The labyrinth is formed of finely fibrous and mesenchyma-like tissues which may, in reptiles as in mammals, be classified on a regional basis as: (1) the *membrana propria,* which forms the intimate fibrous investment of the epithelial otic labyrinth; (2) the *internal periosteum,* which forms the fibrous lining of the otic capsule; and (3) the *periotic reticulum* (Streeter, 1918), loosely arranged or delicately organized connective tissues which extend between the two layers defined and form the spaces containing the periotic fluid.

That part of the periotic labyrinth associated with the superior division of the otic labyrinth is relatively constant in its morphology in the reptiles examined. The utricle is surrounded rather uniformly by periotic reticulum except at the points where it is joined by the semicircular ducts. Here the amount of reticulum is reduced and larger periotic lumina are present; from these areas extend the *periotic ampullae* and *periotic semicircular canals.* The former are transversed by sparse reticulum. The latter are crescentic to uncinate in cross section, confined largely to the lesser curvatures and sides of the otic semicircular ducts, and vary in size and amounts of reticulum present in their courses. Generally speaking, the lumen of the periotic semicircular canal is smallest in its middle third. Because of the uniformity, throughout the forms examined, of this part of the periotic labyrinth, it is not specifically treated in this study; rather, attention has been directed primarily toward the periotic adnexa of the inferior division of the otic labyrinth.

Three fluid compartments have classically been associated with the saccule and cochlear duct in reptiles other than archosaurs. As they are usually described, these are: (1) a large compartment situated lateral to the entire lateral walls of the saccule and cochlear duct, bounded laterally by the otic capsule and footplate of the columella auris, and designated as the perilymphatic cistern; (2) a second compartment, the perilymphatic sac, situated medial to the cochlear duct and usually possessed of diverticula which associate themselves with the cranial cavity and/or some part of the tympanic cavity; and (3) a tubular connection, called perilymphatic duct, which curves around the anterior surface of the cochlear duct to unite the two larger fluid spaces. Diverticula extending from the two larger compartments have been variously named. The material available for this investigation indicates that more specialization may exist in this portion of the periotic labyrinth than has generally been recognized, and that the parts lend themselves to a rather uniform terminology. Retzius (1884), in some cases, suggests similar findings; he does not, however, carry these uniformly through his descriptive material.

The common periotic cavity situated internal to the footplate of the columella auris (Fig. 2) has a relatively consistent relationship to the otic labyrinth. This relationship is, in most forms, restricted to the lateral wall of the proximal (vestibular) end of the cochlear duct, the ductus reuniens and the lateral wall of the saccule adjacent to the ductus reuniens. Two extensions of this cavity can be recognized; one associates itself, primarily, with the remaining part of the lateral wall of the saccule; the other extends along one wall of the cochlear duct. The common cavity plus its saccular extension forms a compartment extremely similar to the space designated vestibule or *periotic cistern* in mammals. The latter term has commonly been applied in the internal ear of reptiles; it seems logical, therefore, to retain it for use in the restricted sense indicated.

The cochlear extension of the periotic cistern is clearly differentiated in archosaurs and more subtly so in most other reptiles; the manner in which it is delimited in each group is described below. In all forms in which it can be recognized, the cochlear extension of the periotic cistern associates itself with the vestibular membrane and extends from the common cavity toward the distal limit of the cochlear duct. This structure in reptiles appears to be at least analogous (if not homologous) to the scala vestibuli of birds and mammals, and has been recognized in archosaurs and some lizards by that term by Retzius (1884), de Burlet (1934) and others. The term *scala vestibuli* is, therefore, applied to the cochlear extension of the periotic cistern.

Application of the term perilymphatic (periotic) duct to the short narrow channel which, at the level of the lagena, connects the scala vestibuli to the periotic compartment situated adjacent to the basilar membrane, does not seem desirable. Such application falsely suggests that this structure is homologous to the mammalian periotic duct. The position, connections and form of this channel suggest that it may be more appropriately called the *helicotrema.*

The periotic compartment associated with the basilar membrane may take the form either of a sac with specialized extensions, or

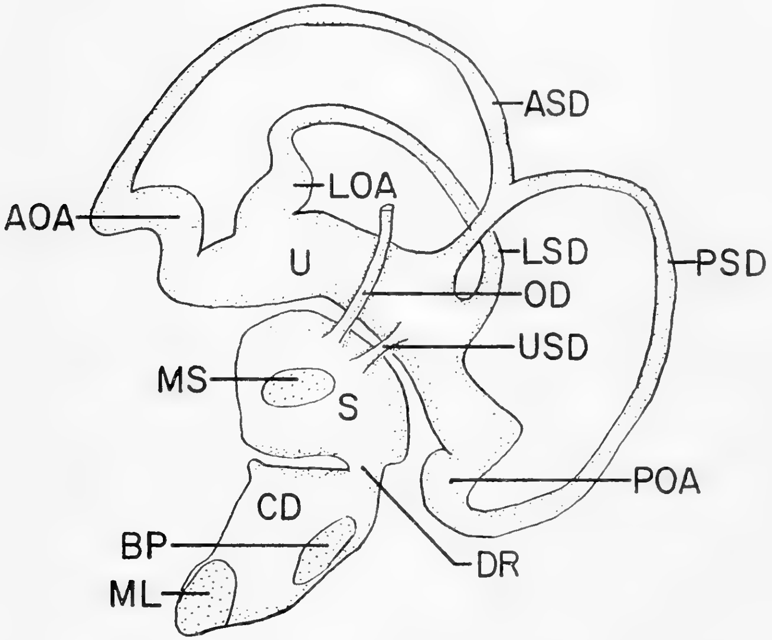

FIG. 2. Diagrams of the inferior divisions of the labyrinths in a "typical" lizard. a—Lateral aspect of left saccule and cochlear duct. c—Lateral aspect of periotic adnexa of same structures e—Lateral aspect of combined otic and periotic parts. b, d and f—Medial views comparable to a, c and e.

one which might be loosely described as flask-shaped; in the latter case the helicotrema opens into a larger duct which extends along part of the medial cochlear wall before terminating in a sacciform enlargement. The elongate duct of the latter case is termed *scala tympani;* the irregular sac of both situations is designated *periotic sac.* Special extensions of the several parts of the labyrinth are described and named in the specific descriptive material.

The otic capsule is composed of the united *prootic* and *opisthotic* bones. *Vestibular* and *cochlear recesses* are recognized as general divisions of the central cavity of the capsule. The terms applied to the foramina of the capsule and adjacent areas are largely those employed by de Beer (1937).

THE SACCULO-COCHLEAR PORTION OF THE PERIOTIC LABYRINTH

RHYNCHOCEPHALIA

Sphenodontidae

(Figs. 3-6; 48)

The auditory region of *Sphenodon* has received attention from an unusual number of workers. Notable contributions to the anatomy of the otic and periotic labyrinths of the species have been made by Retzius (1884), Osawa (1898) and Wyeth (1924). The relationship between the saccule and cochlear duct has been noted by these investigators (and others) to differ somewhat from the typical reptilian condition. The ductus reuniens originates from the medial wall of the saccule just posterior to its midpoint; this connection places the proximal third of the cochlear duct medial to the saccule rather than primarily inferior to that structure, as is common in most other reptiles. This difference in otic relationships, coupled with the fact that only late embryos were examined, may account for some of the complexity of the periotic cistern, noted below.

The major part of the periotic cistern is situated internal to the footplate of the columella auris, and abuts medially against the vestibular membrane of the middle third of the cochlear duct and the inferior part of the lateral wall of the saccule. The axis of this irregular cavity is oblique and corresponds roughly to the anterior margin of the saccule. An extension reaches superiorly from the medial margin of this cavity and lies in the narrow space between the saccule and related lateral wall of the cochlear duct A narrow uncinate extension of the cavity turns medially around the posterior margin of the cochlear duct to end blindly just short of the basilar membrane.

From the anterosuperior aspect of the major cavity, the periotic cistern extends upward about the saccule, investing the anterior half of the medial saccular wall and the greater part of the lateral saccular wall with a narrow periotic space. From the posteromedial aspect of the major cavity (that part situated between the saccule and upper third of the cochlear duct) a second extension passes superiorly, curves laterally around the posterior margin of the saccule and communicates with the lateral saccular periotic space. From the area of union of these two extensions of the major cavity of the cistern, the saccular periotic space reaches superiorly to relate itself to the posterior superior aspect of the saccule. Here it enlarges into a cavity of considerable size. This complex association of periotic spaces, although possibly characteristic of the late embryo rather than of the adult, is considered to comprise the periotic cistern as defined above.

From the anteromedial margin of the inferior limit of the periotic cistern, a discrete, flattened, spiral, periotic channel arises. It extends forward, then turns medially around the anterior margin of the lagena to cross posteroinferiorly over the medial wall of that structure. It terminates by hooking laterally around the posterior lagenar margin and narrowing to form a pointed blind ending. The course of this channel is adjacent to the entire macula lagenae, which appears to constitute its only significant relationship. Similar diverticula of the periotic cistern or scala vestibuli, although not usually as large and clearly defined as that in *Sphenodon* are present in other reptiles. Lagenar extensions or diverticula of the periotic labyrinth are mentioned in the literature, but no specific name appears to have been assigned to them. The term *scala lagenae* is, therefore, suggested as being appropriate for the designation of periotic diverticula which relate themselves to the lagena, and will be used in that sense.

Immediately superior to the origin of the scala lagenae is a narrow anterior extension of the periotic cistern, which associates itself with that portion of the vestibular membrane immediately proximal (superior) to the lagena. This extension is probably homologous to the anterior part of the scala vestibuli of other reptiles, but is not considered to be clearly enough delimited to merit that name in *Sphenodon.* From the superior margin of this extension of the periotic cistern, the helicotrema originates and hooks superomedially to pass above the lagena, then posteroinferiorly to join the superior margin of an anterior extension of the periotic sac. This extension of the sac is probably homologous to the scala tympani of other reptiles, but, like the cisternal extension, it is not clearly demarcated from its parent periotic space. The helicotrema is large in *Sphenodon,* and is not as extensively surrounded by bone as it is in some other reptiles.

The periotic sac bears complex relationships to the otic capsule and cranial cavity. The anterior third of the sac is entirely intracapsular; it rests laterally against the medial wall of the cochlear duct, and is bounded medially by the medial wall of the otic capsule.

The middle third of the sac, situated directly opposite the footplate of the columella auris and related part of the periotic cistern.

is both intracapsular and intracranial. Laterally, this part of the sac contacts the relatively small basilar membrane, limbus and adjacent medial wall of the cochlear duct. Medially, it exits from the otic capsule via the large periotic (perilymphatic) foramen to enter the cranial cavity superior to, and within, the anterior part of the metotic fissure. The sac is large here, fills the greater part of the metotic fissure, and overlaps its margins to become associated with the adjacent cranial wall and floor. The walls of the sac (continuous with the intracapsular periosteum) appear to blend with the intracranial periosteum. I can detect no communication with the cerebrospinal fluid compartment (subarachnoid space of Wyeth, 1924) in this area. On the contrary, the dura mater appears to be reflected over the superomedial aspect of the periotic sac, supplementing its wall and effectively blocking any subdural communication.

The posterior third of the periotic sac is extracranial. It achieves this position by exiting through the vagus (jugular) foramen, situated toward the posterior limit of the metotic fissure, in company with cranial nerves IX, X and XI, and (according to Wyeth, 1924) the posterior cephalic vein. The blindly ending inferolateral extremity of the periotic sac approaches the wall of the pharynx, but remains separated from it by connective tissue and some of the pharyngeal musculature. I can detect no communication with interstitial spaces in this area.

SQUAMATA

Suborder LACERTILIA

Iguanidae

(Figs. 7-14)

In iguanid lizards examined, the saccule and cochlear duct are similar in size and separated along their adjacent surfaces only by a narrow condensation of the periotic reticulum. The saccule is obliquely placed within the vestibular recess; its inferolateral margin slightly overhangs the superolateral margin of the cochlear duct, and is directed toward the superior margin of the fenestra vestibuli. The ductus reuniens leaves the saccule at its posteroinferior margin and immediately joins the posterosuperior angle of the cochlear duct. The latter has the form of a blunted, laterally compressed pyramid, the base of which is directed anteromedially and includes the relatively large lagena.

In the cochlear recess, where it is impinged upon by the footplate of the columella auris, the periotic cistern is laterally compressed and of small capacity. As it extends upward from this area to enter the vestibular recess, it abruptly enlarges to occupy a considerable part of that cavity. The cistern is largest in the area where it abuts against the superolateral surface of the saccule; anteriorly and posteriorly, it extends medially to invest the anterior and posterior walls of that structure.

A scala lagenae is present in all forms of this group examined. The scala appears as an inferiorly-projecting channel which originates from the anteroinferior margin of the periotic cistern (or scala vestibuli) at the level of, or anterior to, the anterior part of the footplate of the columella auris. Considerable variation in the size and form of the scala is present in the family, and this appears to be correlated with the degree of development of the macula lagenae and basilar papilla. For example, in *Anolis,* where the macula lagenae is small and the basilar papilla relatively large, the scala lagenae appears as no more than a minor projection of the periotic cistern; in *Crotaphytus*, where the macula lagenae is large and the basilar papilla is relatively small, the scala is a strong hooked channel which covers considerable portions of the lateral and posterior walls of the lagena. Other genera examined show conditions ranging between these extremes. An analysis of the scala and macula lagenae as they are correlated with degrees of development of other saccular and cochlear receptors is indicated, but is beyond the scope of this paper.

The scala vestibuli originates from the anterior margin of the periotic cistern just anterior to the footplate of the columella, and courses anteriorly along the vestibular wall of the cochlear duct to terminate in a narrow helicotrema. In *Crotaphytus*, *Sceloporus* and *Uta,* the scala vestibuli is short and poorly delimited from the overlying saccular part of the periotic cistern. Such limitation as is present appears to be accomplished by a slight, medially projecting ridge of bone along the anterolateral part of the superior margin of the cochlear recess. In *Anolis* and *Phrynosoma,* in which the scala is relatively longer, the separation of the channel is distinct. This is accomplished by means of a lamina of organized periotic connective tissue, which attaches laterally to the ridge along the anterolateral part of the superior margin of the cochlear recess, and medially to the periotic reticulum separating the adjacent surfaces of the saccule and cochlear duct. In *Anolis,* the ridge and membrane have their posterior limits slightly anterior and superior to the fenestra ovalis (vestibuli); in *Phrynosoma* the posterior margin lies superior to the anterior part of the fenestra ovalis (vestibuli). I have been unable to find reference to this periotic membrane in the literature, although it is shown by de Burlet (1934) in a section from the ear of *Gecko*. It appears to serve primarily as a superior wall for the scala vestibuli, but in other families (described below) the membrane gives the impression of serving as a suspensory structure supporting the inferolateral margin of the saccule. I have called the membrane the *cisternal septum*, and for convenience, shall apply the term here.

From the anterior limit of the scala vestibuli, the helicotrema turns medially around the anterior limit of the cochlear duct and lagena, and is separated from those structures by a heavy layer of periotic reticulum. In all forms examined, the helicotrema is housed in a furrow (recess of the perilymphatic duct of Oelrich, 1956) in the anterior wall of the cochlear recess. This furrow, as indicated by the above investigator, may extend along both medial and lateral walls of the cochlear recess, where it houses parts of the scala tympani and scala vestibuli. My material indicates that the depth of the furrow may vary considerably where it is related to the scalae, and indication of its presence on the external surfaces of the otic capsule may be obscured by the thickness of the bone it traverses.

Medial to the cochlear duct, anterior to the limbus, the helicotrema joins the slightly larger scala tympani. The latter courses posteriorly, inclining inferiorly in *Phrynosoma*, maintaining a practically horizontal course in *Anolis*, and inclining superiorly in the other genera examined. Medially, the scala tympani is housed in an extension of the furrow containing the helicotrema. Laterally, it is related to the limbus and cochlear rami of the posterior division of the auditory nerve. The medial relationships of the scala tympani are more intimate in *Anolis* and *Phrynosoma* than in representatives of the other genera; in the latter, a strip of loose periotic reticulum intervenes between the scala and the more medial structures. In *Anolis* and *Phrynosoma*, furthermore, the terminal part of the scala tympani is in direct contact with the basilar membrane underlying the anterior part of the basilar papilla; this situation does not obtain in other representatives of this family.

The scala tympani terminates by entering the anterosuperior aspect of the periotic sac, the intracapsular part of which is small and in immediate contact with the basilar membrane. Posteroinferiorly, the sac exits from the otic capsule, narrowing slightly as it traverses the periotic (perilymphatic) foramen, then expands within the recessus scalae tympani. The extracapsular part of the periotic sac is large in *Phrynosoma, Sceloporus* and *Uta,* and relatively smaller in *Anolis* and *Crotaphytus.*

Immediately inferior to the periotic foramen, the extracapsular part of the periotic sac is related medially to the dura mater by way of the medial aperture of the recessus scalae tympani, and to the glossopharyngeal nerve, which traverses that aperture. As in other forms, I can detect no free communication between the periotic sac and the cerebrospinal fluid compartment. The dura mater appears, in my material, to form a continuous lamina over the medial extension of the periotic sac, and to clothe the glossopharyngeal nerve in its relationship to the sac. Furthermore, in *Crotaphytus,* injections of 0.5% Evans Blue into the periotic sac filled the periotic labyrinth but did not appear in the cerebrospinal fluid, and conversely, injections of the dye into the cerebrospinal fluid did not appear in the periotic labyrinth. Radiographic examinations (method of Young, 1952) also indicate that the only opening of the periotic sac is that which traverses the periotic foramen. This experimental evidence appears to support microscopic observations and indicates that any communication here between the periotic and cerebrospinal fluids is, at best, by way of a selectively permeable membrane.

From the level of the periotic foramen and medial aperture of the recessus scalae tympani, the extracapsular part of the periotic sac sweeps posteriorly and laterally to occupy part of the cavity termed by Oelrich (1956), in the related genus *Ctenosaura,* the *occipital recess.** The external wall of this part of the sac is fused with the mucosa of the tympanic cavity to form the secondary tympanic membrane. This membrane varies considerably in its relative and absolute size within the family. It is attached to the crista interfenestralis and crista tuberalis along those surfaces which face into the recess, and, except in *Anolis,* rather close to their free margins. In *Crotaphytus,* the secondary tympanic membrane is large, looks anterolaterally into the tympanic cavity and curves posterosuperiorly from the level of the anterior margin of the apertura medialis recessus scalae tympani. *Sceloporus* and *Uta* show a rather similar situation. In *Anolis* and *Phrynosoma,* the secondary tympanic membrane faces inferolaterally and postero-

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* This term appears to be synonymous with the term *recessus scalae tympani* as used by Romer (1956) and others; see discussion.

laterally, respectively, and does not extend significantly posterior to the level of the medial aperture of the recessus scalae tympani.

Eublepharidae

(Figs. 15-16)

In *Coleonyx,* the saccule is distinctly smaller than the cochlear duct and separated from that structure except anteriorly where it slightly overhangs the superolateral margin of the duct. Attached to the central part of the lateral saccular wall is a relatively small, densely organized mass of connective tissue; this is situated opposite the saccular macula and seems to represent an elaboration of the membrana propria. The mass has no other attachments and appears to be maintained in position solely by the surrounding, thin, lateral wall of the saccule. At its posterior limit, the saccule opens freely into the ductus reuniens, which descends to open into the posterior superior angle of the cochlear duct. The latter structure is large, carries a posteriorly-elongated basilar papilla, and has associated with its medial wall a large limbus with a well-developed limbic lip (see Shute and Bellairs, 1953). Otherwise, its structure is similar to that in most other lizards.

The major part of the periotic cistern abuts against the lateral walls of the posterior halves of the saccule and cochlear duct. The cochlear part of the cistern is somewhat narrower than the saccular part, and is in contact laterally with the antero-posteriorly elongated footplate of the columella auris. The saccular part of the cistern extends anteriorly and posteriorly to relate itself to the entire lateral, and the anterior and posterior surfaces of the saccule.

The scala vestibuli forms an anterior extension of the cochlear part of the periotic cistern, and is related to the anterior half of the vestibular membrane. The scala has its posterior limit at the level of the anterior margin of the columellar footplate, above which a distinct medially-projecting ridge of bone arises and extends forward to mark the superolateral margin of the anterior part of the cochlear recess. This ridge, more prominent anteriorly, forms the lateral part of the roof of the scala vestibuli and gives attachment to a cisternal septum, which forms the medial part of the roof. Posteriorly, the septum is formed by a lamina extending solely from the membrana propria of the inferior margin of the saccule; anteriorly, the septum is heavier, and is attached medially to both the membrana propria and the periotic reticulum inferomedial to the saccule.

A narrow periotic diverticulum arises from the superomedial aspect of the scala vestibuli near its posterior limit, and extends superomedially (and slightly anteriorly) between the opposing surfaces of the saccule and cochlear duct. Medial to the saccule, the diverticulum expands into a periotic chamber related to the inferomedial wall of the saccule. This chamber extends primarily rostrally, surrounded except along its saccular surface by periotic reticulum, and is related to the base of the saccular macula. The chamber appears to end blindly just short of the anterior limit of the saccule, but the material available does not allow me to be positive on this point. Although this diverticulum is indirectly related to the superior wall of the cochlear duct and the lateral wall of the utricle, it is most intimately related to the saccule and the base of the saccular macula. I can find no reference to this channel in the literature, and have called it the *scala sacculi*.

A small but distinct scala lagenae is present in *Coleonyx*. Arising from the anteroinferior margin of the scala vestibuli, it reaches along the lateral wall of the lagena to its anterior limit, and extends inferiorly to hook medially below the lagenar floor. Superior to the scala lagenae, the scala vestibuli communicates with the helicotrema. This is, laterally, housed in a deep groove in the lateral wall of the cochlear recess and separated from the cochlear duct by a dense layer of periotic reticulum. As the helicotrema follows its short rostral course, the groove deepens and, at the anterior limit of the cochlear duct, continues into a bony canal in the anterior wall of the cochlear recess. Within this canal, the helicotrema hooks medially, inferiorly and posteriorly. Following this diagonal curved descent, it re-enters the cochlear recess where it lies in a deep groove in the medial wall of the recess, immediately inferior to the foramen transmitting the posterior ramus of the auditory nerve. The helicotrema passes medial to the lagenar ramuli of that nerve, and communicates with the scala tympani at the level of the anterior extremity of the limbus. The latter channel is short; it courses posteriorly, medial to the anterior extremities of the limbus, basilar membrane and basilar papilla, and inferior to the anterior part of the cochlear ganglion. It terminates by entering the periotic sac at the level of the anterior margin of the periotic foramen, opposite the anterior margin of the footplate of the columella auris.

The periotic sac is relatively small in *Coleonyx*. Laterally, it abuts against the central part of the basilar membrane; inferiorly, it extends freely into the recessus scalae tympani by way of a large periotic foramen. The intracapsular part of the sac is extended posteriorly and superiorly in relation to the posterior part of the basilar membrane and papilla by means of a diverticulum. This channel, described by Shute and Bellairs (1953) as "a diverticulum from the perilymphatic sac," occupies a groove in the lateral surface of the limbus and, tapering throughout its course, extends to end blindly at the posterior limit of the basilar membrane and papilla. The posterior limits of all three structures lie opposite the posterior margin of the footplate of the columella auris. Since specialized periotic diverticula are relatively common in the ears of reptiles, it would seem desirable to recognize this channel by a more specific term than has been suggested by those who originally described it; I suggest, therefore, that the term *accessory scala tympani* be used to designate diverticula of this sort.

The extracapsular part of the periotic sac is, anteriorly, poorly delimited from the intracapsular part. This is the result, primarily, of differences in the attachments of the secondary tympanic membrane from those noted in iguanid lizards. Anterolaterally, the membrane attaches to the otic capsule along the external margin of the periotic foramen; posterior to the limit of the foramen, the lateral attachment is to a slight ridge on the inferior surface of the otic capsule. The entire medial attachment is to the basis cranii along a line immediately inferior to the medial aperture of the recessus scalae tympani. These attachments place the secondary tympanic membrane at the depths of the recessus scalae tympani rather than toward its lateral margins, and cause the membrane to face inferiorly into the recess rather than laterally or inferolaterally into the tympanic cavity proper. Thus, in the region of the periotic foramen, the periotic sac is triangular in cross section; superolaterally it contacts the basilar membrane; medially it contacts the meninges via the medial aperture of the recessus scalae tympani; and inferiorly it enters into the formation of the secondary tympanic membrane. Posterior to the periotic foramen, the sac extends posteriorly for a short distance, inferomedial to the otic capsule. In this area it is traversed by the ninth cranial nerve, which exits from the cranial cavity through a foramen situated immediately posterior to the medial aperture of the recessus scalae tympani. As in other forms, no communication between the periotic sac and cerebrospinal fluid compartment could be detected.

Sphaerodactylidae

The structures of the internal ear in *Sphaerodactylus* show remarkable shortening of their antero-posterior axes, accompanied by an apparent increase in their vertical dimensions. This is marked in the saccule and cochlear duct, both of which give the impression of being antero-posteriorly compressed and vertically attenuated. The saccule is additionally modified in that part of its lateral wall, is drawn laterally and, except at its anterior and posterior extremities, firmly attached to the lateral wall of the vestibular recess. The attachment is made by (apparently) an elaboration of the membrana propria in the area corresponding to the position of the connective tissue mass noted in *Coleonyx*. This elaboration extends over, and greatly thickens, the free superolateral wall of the saccule. Thus, only the inferolateral part of the lateral saccular wall is thin, since the inferomedial wall rests upon dense periotic reticulum occupying the narrow space between the cochlear duct and overlapping saccule, and, more dorsally, between the saccule and utricle.

The ductus reuniens is small, and joins the saccule and cochlear duct at their posterior margins. The cochlear duct is smaller than the saccule and neither the limbus nor the basilar papilla shows elongation. The round footplate of the columella auris is situated lateral to the duct, directly opposite and slightly anterior to the basilar papilla.

The major cavity of the periotic cistern lies adjacent to the posterior halves of the vestibular membrane and inferolateral wall of the saccule. In this area, it is rather distinctly divided into saccular and cochlear parts by a ridge of bone which projects superomedially from the lateral superior margin of the cochlear recess; the division is least marked immediately superior to the footplate, where the ridge is lowest. The saccular part of the cistern sweeps superiorly, anterior and posterior to the attached part of the lateral saccular wall, and extends above the area of attachment adjacent to the thick, free, superolateral wall of the saccule. Thus, the saccular part of the periotic cistern forms a roughly circular cavity, which surrounds an axis formed by the saccule and its lateral attachment and communicates ventrally with the cochlear part of the cistern.

The scala vestibuli is short, corresponding to the shortness of the cochlear duct; it originates from the cochlear part of the periotic cistern just rostral to the anterior limit of the columellar footplate. At this level, the ridge along the superolateral margin of the cochlear recess inclines medially, forming the lateral part of the roof of the scala, and gives attachment to a cisternal septum, which extends to the periotic tissue inferomedial to the saccule and forms the medial part of the scalar roof. The scala vestibuli contacts virtually the entire lateral wall of the cochlear duct and lagena, hence, no discrete scala lagenae can be identified. No scala sacculi is present.

Anteriorly, the scala vestibuli terminates abruptly and communicates with the helicotrema, which, at the level of the anterior margin of the cochlear duct, arises as a narrow channel from the superior part of the scala. The helicotrema does not perceptibly groove the wall of the cochlear recess, but passes through dense periotic reticulum and, almost immediately, enters a bony canal in the anterior wall of the cochlear recess. In this canal it hooks medially and descends, then, still in the canal, turns posteriorly along the medial wall of the cochlear recess. The helicotrema terminates medially just anterior to the level of the anterior margin of the columellar footplate, where the bony canal opens into the cochlear recess; here the helicotrema communicates with the scala tympani. The latter is situated ventral to the cochlear ganglion and lies in a groove on the medial surface of the limbus. These relationships are maintained while, expanding in size, the scala traverses a short course posteriorly. At the level of the posterior part of the footplate of the columella, the scala tympani contacts laterally the anterior part of the small basilar membrane. Immediately posterior to this, it terminates in the anterosuperior part of the periotic sac.

The periotic sac is remarkably compact in *Sphaerodactylus*. It is situated posterior to the level of the posterior margin of the footplate of the columella, and contacts no more than half of the basilar membrane. Inferomedially it passes freely through the periotic foramen and occupies the deeper half of a small and poorly-defined recessus scalae tympani. Intra- and extracapsular parts of the sac can be only arbitrarily defined, since the sac is restricted to the small area inferomedial to the periotic foramen. Viewed in transverse section, the sac is triangular; superolaterally it contacts the posterior part of the basilar membrane and adjacent limbus, medially it rests against the dura mater at the medial aperture of the recess, and inferolaterally it fuses with the mucous membrane of the tympanic cavity to form the secondary tympanic membrane. The sac does not extend posterior to the level of the posterior margins of the periotic foramen and medial aperture of the recessus scalae tympani. No communication of the periotic sac with the cerebrospinal fluid compartment could be discerned, and no accessory scala tympani is present in *Sphaerodactylus*.

Gekkonidae

(Figs. 17-20)

In both *Aristelliger* and *Hemidactylus*, the saccule is approximately the same size as the cochlear duct, has approximately equal longitudinal and vertical measurements, and appears to be suspended obliquely in the vestibular recess between two ridges of bone. The inferior ridge is that marking the lateral superior margin of the cochlear recess; the superior ridge arches longitudinally along the vestibular roof from just lateral to the anterior ampulla to just lateral to the posterior ampulla. In *Aristelliger* the inferolateral margin of the saccule actually touches and attaches to the opposing ridge throughout its length. In *Hemidactylus*, a similar relationship is present anteriorly, but, from a short distance anterior to the footplate of the columella to a level just posterior to the mid-point of that structure, the inferolateral attachment of the saccule to the ridge is made by means of a cisternal septum. Additionally, in this form, the central part of the lateral wall of the saccule makes a strong attachment to the superolateral wall of the vestibular recess. This is accomplished by an even greater elaboration of periotic connective tissue than that seen in *Sphaerodactylus*. In the latter, the connective tissue followed the contour of the saccule; in *Hemidactylus* the mass is larger, denser and more highly organized, and gives the impression of infringing upon and reducing the size of the cavity of the saccule. In sectioning, its density produces some disruption in the tissues surrounding it, so that it is impossible to state precisely the relationships of the mass to the saccular wall.

The lateral saccular wall is free and unmodified in adult specimens of *Aristelliger*. Late embryos labelled *A. praesignis* in the Harvard Embryological Collection show a definite contact and weak attachment of the lateral saccular wall to the lateral wall of the vestibular recess, but the organization of the remaining parts of the ear suggests that a remarkable reorganization occurs in the ear postnatally, or during terminal embryonic development.

Like the saccule, the ductus reuniens in *Aristelliger* differs notably from that in *Hemidactylus*. In the latter, the duct is small, short, tubular and extends from the posteroinferior angle of the saccule to the posterosuperior angle of the cochlear duct. In *Aristelliger*, on the other hand, the duct is antero-posteriorly wide, laterally compressed and leaves the saccule posteromedially. It makes a broad communication with the cochlear duct and is associated, medially, with the posterior extremity of the limbus.

The pyramidal cochlear ducts are basically similar in the two forms examined; differences noted do not significantly alter the organization of the associated parts of the periotic labyrinth. The basilar membrane and papilla are elongate in both forms.

Because of the extended inferolateral attachment of the saccule in these gekkonids, the part of the periotic cistern common to the saccule and cochlear duct is confined to those small portions of the vestibular and cochlear recesses which lie posterior to the level of the shaft of the columella auris. This part of the cistern contacts a small part of the lateral wall of the saccule in *Hemidactylus;* it is lateral only to the ductus reuniens and lies posterior to the saccule and cochlear duct in *Aristelliger.* The saccular part of the cistern extends anteriorly in the vestibular recess to form a large compartment, simple and superolateral to the saccule in *Aristelliger,* but encircling the saccular attachment in *Hemidactylus,* much as it does in *Sphaerodactylus.*

The scala vestibuli is related to the entire lateral wall of the cochlear duct in *Aristelliger,* and all but its hindermost extremity in *Hemidactylus.* The footplate of the columella auris, elongate in the former, confines its contact to the scala in that form; in *Hemidactylus,* the round footplate, posterior to the level of its shaft, makes minor contact with the periotic cistern, but the greater part of its area rests against the scala vestibuli.

In both forms a strong scala sacculi is present. In *Hemidactylus,* it arises from the superolateral margin of the scala vestibuli anterior to the level of the anterior margin of the footplate, extends between the opposing surfaces of the saccule and cochlear duct, then expands into a "Y-shaped" compartment, the posterior limb of which is considerably larger than the anterior. Both limbs of this compartment end blindly, and the whole lies against and closely corresponds to the shape of the base of the saccular macula. In *Aristelliger,* a more complex relationship is present. Opposite the entire extent of the footplate, the scala vestibuli extends superomedially in contact with the high lateral wall of the cochlear duct; this extension is related superolaterally to the inferomedial saccular wall, and is continuous posteriorly with the periotic cistern.

At the level of the anterior limit of the footplate, the superior margin of the cochlear duct becomes attached by periotic connective tissue to the inferomedial saccular wall near its lateral limit, leaving a part of the extension of the scala vestibuli confined above the attachment. The channel so formed extends rostrally, lying against the central part of the medial wall of the saccule for its full length, and communicates anteriorly with the saccular part of the periotic cistern in the anterior part of the vestibular recess. A second communication is made between the scala vestibuli and longitudinal part of the scala sacculi posterior to the helicotrema, opposite the anterior part of the limbus. This channel is in a position similar to the single communication noted in *Hemidactylus.* Although the scala sacculi lies at the base of the macula sacculi in *Aristelliger,* it is separated from it by rather dense periotic reticulum, not unlike that which separates it from the utricle and cochlear duct. This differs from the condition in *Coleonyx* and *Hemidactylus* in which there is intimate contact between the scala and base of the macula.

A scala lagenae is present in both forms. It constitutes no more than an inferiorly-directed triangular projection of the anterior part of the scala vestibuli in *Hemidactylus.* In *Aristelliger,* the scala is larger and extends inferiorly from the terminal part of the scala vestibuli and lateral part of the helicotrema. It relates itself not only to the lateral wall of the lagena, but hooks beneath it in contact with its inferior and the lower part of its medial surface, and sweeps anteriorly in contact with the lower part of the anterior surface. Thus, the lagena is virtually ensheathed by the lagenar scala in this form.

The scala vestibuli terminates in the helicotrema just posterior to the anterior limit of the cochlear duct in both forms examined. Occupying a rather shallow groove, the helicotrema hooks medially and inferiorly around the anterior wall of the cochlear recess. It is related to the anterior limit of the cochlear duct and lagena rather closely in this course, and, in *Aristelliger,* is separated from the anterior part of the scala lagenae only by a thin layer of periotic reticulum. Medial to the cochlear duct it passes posteriorly in a canal formed by grooves in the wall of the cochlear recess and anterior part of the limbus; here it passes inferior to the posterior ramus of the auditory nerve and cochlear ganglion, and medial to its lagenar ramuli. In both forms the helicotrema terminates in the scala tympani at the level of the anterior limit of the limbic lip.

The scala tympani is short; it courses posteriorly, related laterally, first to the limbus, then to the anterior part of the basilar membrane and papilla. It achieves the latter relationship just rostral to the level of the anterior margin of the periotic foramen, where it terminates by communicating with the periotic sac.

In *Hemidactylus*, a considerable part of the periotic sac lies anterior to the level of the rostral margin of the footplate of the columella auris. In this area, its immediate relationships are similar to those noted in *Coleonyx* and *Sphaerodactylus;* specifically, it rests against the basilar membrane superolaterally, and extends through the periotic foramen into the superomedial part of the recessus scalae tympani, where it is in contact with the dura mater medially and secondary tympanic membrane inferiorly. Opposite the anterior part of the footplate, the medial aperture of the recessus and the periotic foramen are closed, and the sac occupies an extracapsular position inferomedial to the posterior part of the otic capsule. Facing inferiorly into the recessus scalae tympani, it extends posteriorly in this position only to the level of the shaft of the columella, opposite which it is crossed medially by the ninth cranial nerve. The latter exits from the cranial cavity by way of a small foramen immediately posterior to the medial aperture of the recessus scalae tympani.

In *Aristelliger* the anterior limits of the periotic sac and foramen lie opposite the rostral extremity of the footplate of the columella. At precisely the same level, an extremely narrow vertical slit in the bony wall of the cranial cavity places the periotic sac in contact with the meninges. It is possible that this slit represents a reduced medial aperture of the recessus scalae tympani, for the relationships of the periotic foramen and sac to it are identical with those noted in other gekkonoids. For a short distance posterior to this opening, the wall of the cranial cavity is complete, and the periotic sac rests against bone medially, the basilar membrane superolaterally and the secondary tympanic membrane inferiorly. At the level of the anterior surface of the shaft of the columella auris, the periotic foramen closes and a second foramen appears in the cranial wall medial to the periotic sac. This large opening anteriorly transmits the ninth cranial nerve and allows contact of the extracapsular part of the periotic sac with the dura for a considerable distance. After traversing the foramen, the ninth nerve, superomedial to the periotic sac, courses caudally to the level of the posterior margin of the footplate, where the sac has its posterior limit. The entire secondary tympanic membrane, which faces inferiorly into the recessus scalae tympani, is thick and heavily pigmented. In neither form does the periotic sac appear to communicate with the cerebrospinal fluid compartment.

In both forms an accessory scala tympani arises from the posterosuperior aspect of the intracapsular part of the periotic sac. It inclines posterosuperiorly, occupies a groove in the lateral surface of the limbus and laterally abuts against the posterior part of the basilar membrane. In *Hemidactylus,* the accessory scala extends from the level of the anterior part of the footplate to the level of its posterior margin; in *Aristelliger,* the accessory scala is shorter and lies opposite only the central part of the elongate footplate.

Teiidae

(Figs. 21-23)

The saccule, smaller than the cochlear duct in *Cnemidophorus,* is placed obliquely in the vestibular recess with its superior margin inclined distinctly medially. This is more marked posteriorly where the saccule forms an angle of approximately ninety degrees with the vertical posterior part of the cochlear duct. The inferomedial wall of the saccule is thickened, particularly posteriorly, by a layer of dense periotic connective tissue resembling that of the limbus. Throughout the length of the saccule, the lateral part of this layer touches and attaches to the thick superior wall of the cochlear duct, and, posteriorly, blends into the posterior part of the limbus.

Precise delimitation of the ductus reuniens is difficult because of the intimate association of the adjacent surfaces of the saccule and cochlear duct. Arising as an inferolateral extension of the posterior extremity of the saccule, it is short, duplicates the obliquity of the posterior part of the saccule, and joins the medial aspect of the posterosuperior extremity of the cochlear duct. The latter extends anteroinferiorly in the cochlear recess past the anterior limit of the saccule. Posteriorly, in the region of its association with the limbus, the vertical and transverse dimensions of the duct are considerably smaller than they are anteriorly in the region of the lagena. The basilar membrane and limbic opening housing it take the form of ovals, the long axes of which are vertical; they are situated directly opposite the footplate of the columella auris.

The periotic cistern is large and occupies approximately the lateral halves of both the vestibular and cochlear recesses. The cochlear part of the cistern is narrower than the saccular part, but is in free communication with the latter throughout its contact with the lateral wall of the cochlear duct. The anteroinferior margin of the cistern extends inferiorly as the scala lagenae, but this structure is short and poorly demarcated from the general cavity.

The helicotrema is small and arises from the anterior margin of the periotic cistern adjacent to the anterosuperior margin of the lagena. It turns medially in a shallow groove in the anterior wall of the cochlear recess, then posteriorly along the medial wall, where the groove becomes shallower and disappears at the level of the anterior margin of the posterior acoustic foramen. The medial limb of the helicotrema is related laterally to the dense periotic reticulum of the medial lagenar wall and to lagenar ramuli of the eighth nerve. It passes inferior to the posterior acoustic foramen and terminates in the scala tympani at the level of the posterior margin of that foramen and anterior extremity of the limbus. In contact with the cochlear ganglion superiorly, the scala tympani expands inferolaterally into limbic tissue and empties into the periotic sac superior to the rostral margin of the periotic foramen.

The intracapsular part of the periotic sac forms a transversely-narrow, inferolaterally-expanded, blind ending to the scala tympani. It is short antero-posteriorly, corresponding to the erect oval shape of the basilar membrane, which it touches laterally. Bounded superiorly by limbic tissue and a laterally-directed lip on the superior margin of the periotic foramen, the sac extends medially (and slightly inferiorly) through that foramen. Directed toward the cranial cavity, the extracapsular part of the sac rests against the dura mater and, opposite the root of the glossopharyngeal nerve, bulges strongly through the medial aperture of the recessus scalae tympani toward the brain. Inferolaterally, the wall of the periotic sac enters into the formation of the secondary tympanic membrane. The latter, narrower anteriorly than posteriorly, stretches between the inferior margin of the medial aperture of the recessus scalae tympani and the lateral margin of the periotic foramen. Thus, the extracapsular part of the periotic sac is confined in the superomedial part of the recessus scalae tympani and the secondary tympanic membrane faces into the unoccupied part of the recess; the latter forms a broad shallow fossa in the inferior part of the medial wall of the tympanic cavity. The glossopharyngeal nerve traverses the medial aperture of the recessus scalae tympani, passing inferior to the central part of the periotic sac, and courses posteriorly in this fossa.

Scincidae

(Figs. 24-28)

The following description is based primarily upon the conditions found in the two species of *Eumeces* investigated. The specimen of *Lygosoma* available to me showed some disruption in the intracapsular structures, and although it appears to agree in essential features, it does not offer a firm basis for detailed analysis.

The gross form and relationships between the saccule and cochlear duct do not differ radically from the conditions described in iguanids. The saccule is, relative to the cochlear duct, larger in size than in the Iguanidae and projects laterally more markedly than in that family. The limbus, basilar membrane and basilar papilla show modification in that they are elongated anteroinferiorly in their relationship to the medial cochlear wall.

The periotic cistern has a form similar to that described in iguanid lizards except that there is less distinction between the saccular and cochlear parts. That part of the cistern impinged upon by the footplate of the columella auris appears in cross section as a triangular downward projection of the saccular portion, and is related only to the posterior part of the cochlear duct. From this region, the cistern extends superiorly and anteriorly, becomes larger, and relates itself to the saccule, except along its inferomedial surface.

Just anterior to the fenestra vestibuli, a well-defined cisternal septum extends from the periotic reticulum medial to the saccule and, apparently, from the membrana propria of the saccule itself, to a ridge marking the anterolateral part of the superior margin of the cochlear recess. This septum forms the superior wall of the scala vestibuli, which extends anteromedially and inferiorly, related to the vestibular wall of the cochlear duct. Laterally, the scala is bounded by the wall of the otic capsule. Anteriorly, the scala vestibuli gives rise to a clearly differentiated scala lagenae, which extends inferiorly to abut against the lateral and anterolateral surfaces of the lagena.

The helicotrema arises from the anterosuperior extremity of the scala vestibuli, and turns medially and inferiorly to cross the anterior limit of the cochlear duct superior to the lagena. The helicotrema is lodged in a deep furrow in the bone of the anterior wall of the cochlear recess.

The scala tympani courses posteriorly, traversing a shallow groove in the medial wall of the cochlear recess. In its course, it is related laterally and sequentially to the cochlear rami of the auditory nerve, the cochlear ganglion and limbus, and to the limbus alone; it does not relate itself to the basilar membrane. The scala tympani terminates by entering the anterosuperior aspect of the periotic sac approximately at the level of the anterior margin of the footplate of the columella auris.

The intracapsular portion of the periotic sac lies low in the posterior part of the cochlear recess directly opposite the footplate of the columella auris. It abuts, laterally, against the posterior part of the basilar membrane and, posteroinferiorly, exits from the otic capsule by way of the periotic foramen.

The intracapsular part of the periotic sac gives rise to a vermiform channel or diverticulum, which extends anteroinferiorly, as far as the lagena, in relation to the anterior part of the basilar membrane. The channel is accommodated by a hollowing out of the limbus medial to the basilar membrane; thus, a thin layer of limbic tissue separates the channel from the medial wall of the otic capsule. A periotic channel similar to this has been noted and partially described by Retzius (1884) in *Eumeces (Plestiodon)* and in the related genera *Acontias* and *Egernia.* The author terms the channel the "scala tympani" (his quotes) and states that it may communicate with a periotic space related to the lagena. I have been unable to detect the latter communication in *Eumeces*, but have a few specimens in which disruption of structures could lead to this interpretation. The primary part of the channel, that related to the basilar membrane, does not appear to be the homolog of the accessory scala tympani of the gekkonoids; it is, however, sufficiently similar to that structure in morphology and apparent function that, by analogy, I recognize it by the same name.

The extracapsular part of the periotic sac is related, via the medial aperture of their recessus scalae tympani, to the dura mater, and as in other families, shows no communication with the cerebrospinal fluid compartment. The glossopharyngeal nerve, as noted in some specimens of *E. quinquelineatus* by Rice (1920) and de Beer (1937), relates itself to this part of the sac via a separate foramen (foramen glossopharyngei internum). The interpretation of the latter author agrees with my material, for the course of the nerve appears to be distinctly outside the confines of the cavity of the otic capsule, but does traverse an inferior extension of its medial wall. This course was noted in all specimens of both *Eumeces fasciatus* and *E. obsoletus.*

The extracapsular part of the periotic sac expands posteriorly and laterally beneath the posterior part of the otic capsule, where it occupies the recessus scalae tympani completely. At the lateral aperture of the recess, the inferolateral wall of the periotic sac joins the tympanic mucosa to form the secondary tympanic membrane. The latter is relatively (and probably absolutely) larger in *E. fasciatus* than it is in *E. obsoletus.*

Lacertidae

Figs. 29-31

The organization of structures of the inner ear in *Lacerta* has been covered, or touched upon in part, by an unusual number of investigators (Clason, 1871; Hasse, 1873 a & b; Retzius, 1884; Gaupp, 1900; de Burlet, 1934; and others) and is frequently cited as exemplary of the saurian inner ear. Of the more detailed coverages, that of Retzius is particularly complete, and my own observations on the otic labyrinth and capsule in *Lacerta muralis* and *L. vivipara* agree in practically all basic features with his in *L. viridis* and *L. ocellata.* Separte consideration of these parts is, therefore, omitted.

The periotic cistern is small and restricted almost exclusively to small parts of the lateral surfaces of the cochlear duct and saccule posterior to the level of the footplate of the columella auris. Little, if any, periotic fluid is associated with the lateral and superolateral surfaces of the greater part of the saccule, for, in adult specimens, that organ is expanded and, except at its anterior and posterior extremities, occupies the lateral two-thirds of the vestibular recess. Its lateral and superolateral surfaces are in contact with the wall of the recess, and the membrana propria is closely attached to the internal periosteum. [This differs from the conditions described by Retzius and some others. Their observations may well have been made on embryos, however, for several late embryos of *L. muralis* in the Harvard Embryological Collection show the periotic cistern extending over the lateral and superolateral surfaces of the saccule (Figs. 29-31) in the manner those investigators describe.]

From the small posteriorly-placed cistern, the scala vestibuli extends rostrally, lateral to the cochlear duct and lagena, and is impinged upon by the footplate of the columella auris. The greater part of its roof is formed by the inferior part of the expanded wall of the saccule, but anteriorly, where the saccule is somewhat smaller and shows a small periotic space along its inferolateral surface, a short cisternal septum extends from the membrana propria of the inferomedial saccular wall to the superior lateral margin of the cochlear recess and forms the scalar roof. In the same area, a space exists between the superior surface of the lagena and the opposing surface of the saccule; through this, a scala sacculi extends superomedially from the scala vestibuli and expands into a channel in contact with the inferomedial surface of the saccule. Although it extends to communicate with periotic spaces anterior and posterior to the saccule, the scala sacculi is distinct and unobstructed only where it is related to the base of the macula sacculi; anterior and posterior to this region, it is transversed and made less distinct by loosely organized periotic reticulum. In addition to the scala sacculi, a small scala lagenae arises and extends inferiorly from the anteroinferior margin of the scala vestibuli in both species examined.

The helicotrema is relatively large at its origin from the anterior extremity of the scala vestibuli and as it grooves the anterior wall of the cochlear recess in passing medially around the anterior extremity of the lagena. Medial to the lagena, where it is housed in a deep furrow in the medial wall of the cochlear recess, the diameter of the helicotrema is reduced and remains so posteriorly to the level of the anterior extremity of the limbus. Here the helicotrema continues into the scala tympani. The latter is short, but expands rapidly as it crosses the anterior part of the limbus, and, in *L. muralis,* medially touches the anterior part of the basilar membrane before terminating in the anterosuperior part of the periotic sac.

Small in both species, the intracapsular part of the periotic sac is in contact with the basilar membrane and posterior part of the limbus laterally, and extends freely downward through the periotic foramen. It is interesting to note that, in *L. muralis,* the intracapsular part of the sac is situated posterior to the level of the posterior margin of the footplate, while in *L. vivipara,* it lies directly opposite the footplate. Despite this difference, however, a line extended, in either species, from the center of the footplate through the center of the periotic foramen, passes through the central part of the basilar papilla.

Inferior to the periotic foramen, the extracapsular part of the periotic sac expands to occupy the recessus scalae tympani. Medially, it rests against the dura mater at the medial aperture of the recess, and, at the lateral aperture of the recess, it fuses with the mucosa of the tympanic cavity to form the secondary tympanic membrane. The latter is attached superiorly along, and for a short distance posterior to, the lateral margin of the periotic foraman, and, inferiorly, to the basis cranii. The membrane is larger than the footplate (considerably so in *L. vivipara*) and faces laterally into the tympanic cavity. Its anterior limit lies inferior to the anterior margin of the footplate in *L. vivipara*, and inferior to the posterior margin of the same structure in *L. muralis*. In both species, the posterior limit of the membrane and extracapsular part of the periotic sac is reached at the level of the posterior extremity of the vestibular recess. The glossopharyngeal nerve traverses the posterior part of the medial aperture of the recessus scalae tympani and courses medial to the posterior part of the extracapsular extension of the periotic sac. No communication of periotic with cerebrospinal fluid cavities could be discerned.

Anguidae

(Figs. 32-34)

The saccule in *Ophisaurus* is markedly larger than the cochlear duct. Its anterior third extends rostral to the anterior limit of the lagena, and is housed, with the utricle, in the anterior part of the vestibular recess. This part of the saccule exaggerates the medial inclination of the superior margin shown by the remainder of organ, and is situated superolateral to the utricle. The entire superomedial saccular margin is attached to the vestibular roof by an extension of its membrana propria. The medial saccular wall, except in the region occupied by the macula, rests upon a layer of dense connective tissue resembling that of the limbus. Thickest toward the inferolateral saccular margin, the layer of connective tissue is attached anteriorly to the floor of the vestibular recess, and, posteriorly, blends with the superior margin of the posterior part of the limbus. As this union is approached, the posterior part of the saccule tapers slightly and, inferomedially, enters into the formation of a short laterally-compressed ductus reuniens; the latter appears to be a coalescence of the saccule and cochlear duct rather than a discrete structure. Associated with the medial wall of the ductus are the posterior extremities of the limbus and the saccular connective tissue layer noted above.

The cochlear duct extends anteroinferiorly from the ductus reuniens, its superior margin paralleling and immediately inferior to the inferolateral margin of the saccule; it occupies a relatively shallow cochlear recess. The lagena constitutes approximately the terminal half of the structure and is transversely expanded, relative to the posterior part. Both the basilar papilla and the heavy limbus are slightly elongated, and the latter shows a distinct ridge on its lateral wall above the opening for the basilar membrane, in the position occupied by the limbic lip in gekkonoids.

The periotic cistern is large in *Ophisaurus;* it occupies the space in the vestibular and cochlear recesses lateral to, and along virtually the entire lengths of, the saccule and cochlear duct, including the lagena. The superior part contacts the thin superolateral wall of the saccule and extends medially at the anterior and posterior margins of that structure. Extending between these extremities, a channel passes longitudinally, medial to the saccule and in contact with its medial wall. Some diffuse periotic reticular tissue traverses the channel except at the base of the saccular macula; at that level it makes an additional communication with the major part of the cistern by way of the narrow opening between the adjacent walls of the saccule and cochlear duct. This series of channels resembles a scala sacculi, but it is here less clearly defined than in forms in which the term has been applied previously.

The inferior (cochlear) part of the periotic cistern is transversely narrowed; this is pronounced anteriorly and, just short of the anterior limit of the cochlear recess, a slight ridge of bone projecting medially from the superior lateral margin of the recess slightly constricts the saccular from the cochlear part of the cistern. The division is indistinct, however, and since no cisternal septum is present, no definitive scala vestibuli can be recognized. In the posterior extremity of the cochlear recess, opposite the ductus reuniens and posterior part of the cochlear duct, the periotic cistern is impinged upon by the elongate footplate of the columella auris.

The helicotrema originates directly from the periotic cistern in the rostral part of the cochlear recess. It arises immediately inferior to the ridge mentioned above and, grooving the anterior wall of the cochlear recess, curves medially, then posteriorly around the anterior extremity of the lagena. Projecting inferiorly from its lateral part is a small uncinate scala lagenae, which makes complete the contact of periotic fluid with the lateral surface of the lagena. Medially, the helicotrema is small and passes posteriorly, confined within a deep groove in the medial wall of the cochlear recess. It passes medial to the superior part of the lagena and lagenar ramuli of the posterior division of the auditory nerve. At the level of the anterior limit of the limbus, the helicotrema may be considered to terminate in the scala tympani, which expands laterally into a groove in the limbus. The scala itself is short and makes no contact with the basilar membrane; it terminates in the anterosuperior part of the periotic sac at the level of the anterior margin of the periotic foramen, opposite the anterior margin of the footplate of the columella auris.

The intracapsular part of the periotic sac is relatively small and constitutes a short vertically-expanded continuation of the scala tympani. Its posterior limit is opposite the posterior surface of the shaft of the columella auris. Superolaterally it is in contact with the basilar membrane and part of the limbus; inferomedially it abuts against the medial wall of the otic capsule. Extending posterolaterally and inferiorly through the periotic foramen, the intracapsular part of the sac continues into the expanded extracapsular part, the anterosuperior portion of which is housed in a furrow in the inferior surface of the posterior part of the otic capsule. Inferior and medial to the periotic foramen, and extending slightly caudal to its posterior limit, the extracapsular part of the periotic sac is related intimately to the meninges at the extremely large medial aperture of the recessus scalae tympani and, although possibly artefact, appears to bulge into the cranial cavity. Laterally, the extracapsular part of the sac fills the recessus scalae tympani and, at the lateral aperture of the recess, enters into the formation of the large secondary tympanic membrane, which forms part of the medial wall of the tympanic cavity. The membrane is situated inferior to the footplate and, tapering posteriorly, extends caudal to that structure to the level of the ampulla of the posterior semicircular canal. The membrane is crossed laterally by an artery, probably the internal carotid, and the posterior part of the periotic sac is related medially to the glossopharyngeal nerve.

Varanidae

(Figs. 35-37)

In approximately the posterior two-thirds of the otic capsule, the relationship of the vestibular to the cochlear recess is, in *Varanus,* much as it is in iguanid lizards; the two form a common chamber posteriorly, and are partially demarcated more anteriorly by a ridge of bone extending medially from the lateral superior margin of the cochlear recess. In the anterior third, however, the vestibular and cochlear recesses are separated by a horizontal plate of bone extending between them.

The saccule, roughly quadrangular when viewed from its superolateral aspect, extends rostrad into the anterior part of the vestibular recess for approximately one-fourth its own length. Here it is placed obliquely, its inferolateral margin attached to the floor of the recess and its superolateral margin attached to the roof. These attachments are made by the membrana propria, and are continued posteriorly, caudal to the dividing plate of bone, for approximately half the length of the saccule. The superior attachment continues along the medial part of the roof of the vestibular recess, and the inferior along the ridge of bone marking the lateral superior limit of the cochlear recess. Both the ridge and saccular attachment are absent caudal to the level of the posterior margin of the posterior acoustic foramen. Caudal to this level, the saccule becomes more nearly vertical, tapers posteriorly and, posteromedially, blends into a wide laterally-compressed ductus reuniens. The latter can only arbitrarily be designated, for in fact, it houses the posterior extremities of the saccular macula and basilar papilla, and is closely associated with the posterior part of the limbus.

The cochlear duct extends anteroinferiorly and slightly medially from its communication with the saccule. It is long and laterally compressed except at its lagenar extremity, which is somewhat expanded medially. A heavy limbus is associated with the medial wall of the duct and blends into only slightly less dense periotic reticulum associated with the medial wall of the lagena. The basilar membrane and papilla are elongate, and superior to these structures, a low laterally-projecting ridge of limbic tissue supports a long tectorial membrane.

That part of the periotic cistern common to the saccule and cochlear duct extends rostrad from the posterior limit of the vestibular and cochlear recesses to the level of the posterior limit of the lateral attachment of the saccule. Medially it contacts the posterior parts of the saccule and cochlear duct, and the ductus reuniens. Laterally, the transversely-narrowed, inferior part of the cistern is impinged upon by the triangular footplate of the columella auris. The saccular part of the cistern extends anteriorly, superolateral to the saccule, past the anterior limit of that structure. The cochlear part of the cistern extends anteriorly, beyond the posterior limit of the lateral saccular attachment, as the scala vestibuli.

The exact limits of the scala vestibuli are difficult to determine in *Varanus*, and must be designated rather loosely. Laterally, the channel is clearly defined, posteriorly, by a short cisternal septum extending from the inferolateral margin of the saccule to the ridge along the superior margin of the cochlear recess, and, more anteriorly, by direct contact of the saccule with that ridge. Because of the lateral extension of the saccule, however, its inferomedial wall forms part of the roof of the scala vestibuli as the latter extends superomedially in contact with the vestibular membrane. Furthermore, from the anterior part of the periotic cistern and the adjacent posterior part of the scala vestibuli, a periotic channel extends superomedially, past the superior margin of the cochlear duct, in contact with the remainder of the inferomedial wall of the saccule. This channel strongly resembles the scala sacculi noted in the gekkonoids, particularly that of *Aristelliger*, for here also, it extends anteriorly and communicates with the periotic cistern anterior to the saccule.

Anteriorly, just short of the bony division of the vestibular and cochlear recesses, the scala vestibuli terminates in the helicotrema. This channel is large and represents only a slight reduction in size from that of the scala vestibuli; it is housed in a wide shallow groove as it curves medially around the anterior margin of the cochlear duct, in contact with that structure. Laterally, the terminal part of the scala vestibuli and the helicotrema give off a scala lagenae, which extends inferiorly to contact the entire lateral wall of the lagena. Medially, the helicotrema follows a short course posterosuperiorly, passing between the medial wall of the cochlear recess and anterior parts of the cochlear duct and limbus. At the level of the caudal margin of the posterior acoustic foramen, inferior to the posterior part of the cochlear ganglion, it terminates in a short scala tympani. The latter enlarges abruptly by expanding laterally to occupy a channel in the limbus, and abuts against the anterior part of the basilar membrane. Upon reaching the anterior margin of the periotic foramen, the scala tympani may be considered to terminate in the periotic sac.

A constriction in the area where it traverses the periotic foramen rather clearly defines intra- and extracapsular parts of the periotic sac. The intracapsular part is an expanded prolongation of the scala tympani. It rests medially against the inferior part of the medial wall of the cochlear recess, and, laterally, is in contact with parts of the limbus and the basilar membrane. Posteriorly, the intracapsular part of the sac extends superiorly, following the steep ascent of the basilar membrane toward the ductus reuniens. Caudal to the posterior margin of the periotic foramen, a diverticulum of the sac continues in relationship to the basilar membrane. This diverticulum is similar to the accessory scala tympani of gekkonoids, and I recognize it by the same name. As in the other group, it occupies a groove in the lateral surface of the limbus while, tapering, it abuts against the basilar membrane to the posterior limit of that structure.

Immediately inferior to its exit from the periotic foramen, the extracapsular part of the periotic sac is related medially to the small medial aperture of the recessus scalae tympani. In *Varanus* the latter contains a considerable amount of loose connective tissue and the periotic sac is, therefore, separated from the dura mater rather than in contact with it. The glossopharyngeal nerve exits from the cranial cavity through this opening and courses posteriorly, passing medial to the extracapsular part of the sac. The part of the sac related to the two foramina is small; from this region, it expands laterally and posteriorly within the recessus scalae tympani and extends to the medial wall of the tympanic cavity. Here it fuses with the mucous membrane to form a large triangular secondary tympanic membrane located immediately inferior to the footplate of the columella auris. The membrane is crossed diagonally by an ascending artery of medium size. This vessel is probably the internal carotid artery, but it cannot be traced far enough in my material to verify this identification.

Suborder OPHIDIA

Colubridae

(Figs. 38-41; 50)

Form and organization are rather constant in the otic labyrinths of the colubrids investigated, and are essentially similar to conditions described by Retzius (1884) in several other ophidians. The saccule, considerably larger than the cochlear duct, is oriented obliquely in the vestibular recess with its superior margin inclined distinctly toward the median plane. The inferolateral border of the saccule touches and attaches to the superior surface of the cochlear duct throughout most of the length of the latter, but does not significantly overhang the lateral surface of that structure. The membrana propria of the inferomedial saccular wall is thick, and a lamina of periotic connective tissue extends superomedially from it to attach to the roof of the vestibular recess. Anteriorly, the saccule extends rostral to the cochlear duct and is housed, with the utricle, in the anterior part of the vestibular recess; here, it is attached ventrolaterally, either by direct contact of the inferomedial membrana propria with the vestibular floor, or by a periotic membrane extending between the two structures. Superior to the anterior part of the cochlear duct, a lateral saccular attachment is made by a cisternal septum, which extends from the membrana propria to attach along a slight longitudinal ridge on the internal surface of the elongated anterior part of the footplate of the columella auris. Posteriorly the saccule tapers, narrows and grades into the short elliptical ductus reuniens, which descends to merge with the posterior extremity of the cochlear duct.

Erect in the broad shallow cochlear recess, the cochlear duct extends anteriorly from the ductus reuniens and curves slightly medially toward its anterior extremity. The posterior part of the duct (*pars basilaris cochleae* of Retzius) has the form of an irregular cone, the base of which expands anteroinferiorly toward the lagena; the latter constitutes slightly more than the anterior half of the cochlear duct. The limbus is "C-shaped" and extends to associate itself with part of the lagena as well as with the basal part of the cochlear duct. The vestibular membrane extends between the lateral open arms of the structure, facing the inferior half of the footplate laterally, and the basilar membrane and lagenar macula medially.

The major cavity of the periotic cistern abuts against the lateral surfaces of the ductus reuniens and the posterior extremities of the saccule and cochlear duct. It is impinged upon posteriorly and inferolaterally by the posterior half, approximately, of the footplate of the columella auris, and extends anteriorly along the superolateral surface of the saccule. Excluded from the cochlear recess by the cisternal septum, the saccular extension of the cistern is in contact, inferolaterally, with the superior part of the anterior extremity of the footplate, and extends past the anterior margin of that structure into the anterior extremity of the vestibular recess.

The scala vestibuli arises from the anterior margin of the cochlear part of the periotic cistern opposite the anterior margin of the basilar membrane. This level marks the posterior limit of the cisternal septum, which forms the major part of the scalar roof and separates the scala from the overlying saccular part of the periotic cistern. Approximately triangular in cross section and tapering anteriorly, the scala vestibuli extends rostrad in contact with the thin superior part of the lateral wall of the lagena. It rests, laterally, against the inferior part of the anterior extremity of the footplate, and terminates in the helicotrema just rostral to the anterior margin of the fenestra ovalis (vestibuli). Neither scala lagenae nor scala sacculi can be identified in any of the forms investigated.

Originating as a direct continuation of the scala vestibuli, the helicotrema is situated in a distinct groove in the lateral, anterior and medial walls of the rostral extremity of the cochlear recess. In this location it hooks medially around the anterior extremity of the lagena and comes to lie in the dense periotic tissue adjacent to the superomedial margin of that structure. The medial limb of the helicotrema extends caudally, directly opposite the scala vestibuli, for the full length of the lagena. In this part of its course it passes medial to lagenar ramuli of the posterior division of the auditory nerve, and inferior to the nerve itself. It terminates in the scala tympani at the level of the caudal margin of the posterior acoustic foramen.

Throughout its course in the cochlear recess, the scala tympani is housed in an enlarged extension of the groove accommodating the helicotrema. At its origin from the latter, the scala expands laterally into limbic tissue and touches the basilar membrane; variable vertical enlargement, corresponding to the vertical dimension of the basilar membrane, also occurs but is not great in any of the forms examined. In contact with the full length of the basilar membrane, the scala tympani passes medial to the basilar part of the cochlear duct, and courses beyond it to the inferomedial part of the posterior extremity of the cochlear recess. Here it exits from the otic capsule via the periotic foramen; actually forming a short canal in the forms investigated, the foramen opens caudally into the superior aspect of the recessus scalae tympani. Within the recess the scala tympani terminates in the periotic sac, which is entirely extracapsular.

Although the term "recessus scalae tympani" appears rather regularly in descriptions of the auditory region in ophidians, there appear to be divergences of opinion concerning the relationships, extent and limitations of the structure. For reasons of clarity, therefore, it seems desirable to define the manner in which it is used here, and to describe briefly its relationships to auditory structures in the forms examined. Medially, the posteroinferior relationships of the otic capsule do not differ radically from those in lizards. The periotic foramen, although placed more posteriorly than in most lizards, opens into a recess representing the anterior part of the metotic fissure; the recess communicates with the cranial cavity via an opening traversed by the glossopharyngeal nerve. These structures undoubtedly represent part of the recessus scalae tympani and its medial aperture.

The lateral aperture of the recess is considerably altered by modifications in the position and structure of the fenestra ovalis (vestibuli). Articulated in the fenestra, which is in the posterolateral aspect of the otic capsule, the external surface of the footplate faces inferolaterally, its inferior margin approaching the median plane of the cochlear recess. Encircling the footplate is a crest of bone (Fig. 38) elaborated by the prootic and opisthotic (fused with the exoccipital). The posteroinferior part of this *circumfenestral crest,* formed by the opisthotic, crosses the usual lateral aperture of the recessus scalae tympani and divides it into two openings. One looks posteriorly into the posterior part of the old metotic fissure; through this, the glossopharyngeal nerve exits from the recessus scalae tympani and joins the vagus nerve, with which it exits through the vagus foramen. The second opening faces anterosuperiorly and connects the recess with the fossa formed external to the footplate by the circumfenestral crest.

That part of the periotic sac occupying the recessus scalae tympani is small, since the restricted nature of the recess allows for expansion to a size only slightly greater than the diameter of the scala tympani. Medially, the sac is in contact with the dura mater at the medial aperture of the recess; the area of this contact is small in *Thamnophis, Diadophis* and *Lampropeltis.* In *Carphophis,* the area of contact and the medial aperture are, relatively, much larger, but neither in this genus, nor in the others, is any communication discernable between the periotic and cerebrospinal compartments.

At the lateral extremity of the recessus scalae tympani, the periotic sac turns anterosuperiorly and, traversing the second opening described above, enters the fossa situated lateral to the footplate and encircled by the circumfenestral crest. Here it expands, occupies the fossa fully, and lies against the external surface of the footplate. This terminal expanded part of the periotic sac has been described by de Burlet (1934) as the "pericapsular sinus." For reasons cited below, the term *juxtastapedial sinus* seems more appropriate, and the name *juxtastapedial fossa* might well be applied to the bony cavity it occupies.

Externally, at the mouth of the juxtastapedial fossa, the wall of the sinus is thickened by a fibrous layer and is attached to the circumfenestral crest. The membrane so formed is pigmented and faces the internal surface of the mandibular masculature. In *Thamnophis, Diadophis* and *Lampropeltis* the membrane and the mouth of the juxtastapedial fossa are of approximately the same size as the footplate. In *Carphophis,* however, the size of the membrane and of the mouth of the fossa is reduced to approximately half the area of the footplate by accentuation of the inferior part of the circumfenestral crest; the long narrow membrane in this form faces only the superior half of the footplate.

Chelonia

(Figs. 42-45; 49)

Although two families were represented by the forms investigated, the differences shown in the internal ear do not seem to indicate their separate consideration here. All specimens showed the posterior placement of the cochlear duct, which has been noted repeatedly (Hasse, 1873; Retzius, 1884; de Burlet, 1934; and others), and which considerably affects the organization of the periotic channels.

Situated inferior to the utricle, the saccule lies adjacent to the medial wall of the vestibular recess and opposite the anterior two-thirds of the footplate of the columella auris. The lateral wall of the saccule touches the lateral vestibular wall anterosuperior to the footplate in *Chrysemys*; in *Pseudemys,* a space approximately equal to the width of the saccule intervenes between the two surfaces, and in *Chelydra* the saccule is confined to the medial third of the vestibular recess.

In all forms, the inferior margin of the saccule is attached to the floor of the vestibular recess and, more laterally, to the inferior part of the footplate by rather diffuse periotic reticulum. The attachment to the footplate is elaborated along the posterior margin of the saccule. Here, a lamina of denser reticular tissue extends laterally from the saccular membrana propria and the periotic reticulum between the saccule and cochlear duct; this lamina attaches to the vestibular floor immediately anterior to the bony cochlear recess, and continues laterally to make a narrow vertical attachment to the internal surface of the footplate at the junction of the posterior and central thirds of that structure. Taking the form of a cribrate septum, this laminar attachment essentially completes the separation of vestibular and cochlear recesses inferior to the ductus reuniens. Wever and Vernon (1956) mention attachments of the footplate to the saccule in turtles, and call them "stapedeo-saccular strands." Although this term undoubtedly includes the attachments described above, its authors apparently did not appreciate the definitive form shown by the periotic tissue with which they were dealing. The medial attachments of the cribrate lamina, and its relationships to the parts of the otic labyrinth and to the vestibular and cochlear recesses, are similar to those of the cisternal septum of most lizards; that term (cisternal septum) will, therefore, be used here.

Posteriorly the saccule communicates freely with the cochlear duct by way of a short elliptical ductus reuniens. The cochlear duct extends inferiorly, curving slightly medially toward its inferior extremity. The lagena constitutes approximately the inferior third of the structure and is expanded medially. A heavy limbus is associated with the entire medial wall of the cochlear duct; centrally, it accommodates the basilar membrane.

The large periotic cavity situated lateral to the saccule and cochlear duct is rather definitely limited above, and excluded from contact with parts of the superior division of the otic labyrinth, by a periotic membrane backed by the loosely organized periotic reticulum in which those parts are embedded. Although usually described as a single periotic chamber, the periotic (perilymphatic) cistern, the cavity is actually divided ventrally into two parts by the cisternal septum. This division creates relationships of periotic spaces to saccule and cochlear duct which are quite similar to those noted in most lizards. That part of the cavity anterior to the septum abuts against all (part in *Chrysemys*) of the thin lateral wall of the saccule, and extends posteriorly adajcent to the lateral wall of the ductus reuniens and superior part of the cochlear duct; these relationships make it seem appropriate to restrict the term periotic cistern to the anterior and superior parts of the cavity. That part situated posterior to the cisternal septum abuts against the lateral wall of the cochlear duct (vestibular membrane) and seems to merit the name scala vestibuli. Thus, the anterior two-thirds of the footplate abuts against the saccular part of the periotic cistern; the posterior third of the footplate impinges upon the scala vestibuli. A distinct channel extends ventrally from the scala vestibuli and hooks beneath the lagena in embryos of *Chrysemys*. This channel, which resembles a scala lagenae, is not present in any of the adult turtles examined.

The helicotrema arises from the inferomedial part of the scala vestibuli in the angle formed at the junction of the anterior margin of the lagena with the cisternal septum. It curves anteromedially, traversing the periotic reticulum posteroinferior to the saccule, then, medial to the posterior part of the saccule, inclines anterosuperiorly to a position inferior to the posterior acoustic foramen. Here it forms a genu by turning superiorly, then abruptly posteriorly beneath the cochlear ganglion and lateral to the inferior margin of the posterior acoustic foramen. It extends caudally, embedded in periotic reticulum adjacent to the medial wall of the otic capsule, and passes medial to posterior saccular, cochlear and lagenar ramuli of the posterior division of the auditory nerve. The helicotrema terminates by opening into the scala tympani at the anterior margin of the limbus, opposite the cisternal septum and posterior part of the footplate.

Immediately after its origin, the scala tympani expands laterally and superiorly into limbic tissue and lies against the vertically-oval basilar membrane in the central part of the cochlear duct. The scala narrows somewhat at the posterior limit of the membrane, then continues caudad, embedded in limbic tissue, medial to the posterior part of the cochlear duct. At the posterior limit of that structure, the scala tympani emerges from the limbus and enters the periotic reticular tissue occupying the posterior extremity of the cochlear recess. At this level, it lies immediately inferior to the internal glossopharyngeal foramen, and is crossed superiorly by the glossopharyngeal nerve. Immediately posterior to this, the scala tympani traverses the periotic foramen in the caudal wall of the cochlear recess and terminates in the periotic sac.

The periotic sac is situated in a space termed by Nick (1912) the "ductus hypoperilymphaticus"; the space is further considered by de Beer (1937) who follows Nick in terminology but suggests that, "The cavity of the ductus hypoperilymphaticus would then be merely an enclosed portion of the recessus scalae tympani." Except in that I am unable to find an opening of the space toward the cranial cavity "immediately in front of the jugular foramen" (de Beer, 1937:255), its relationships are as described by that author, and resemble those of the posterior part of the recessus scalae tympani in most other reptiles. It would seem logical, therefore, to apply the term recessus scalae tympani to this space in chelonians, realizing in so doing that it represents only part of the homologous structure in other reptiles.

Expanding within the recess, the periotic sac extends posteriorly to the level of the posterior margin of the vagus (jugular) foramen, where it ends blindly. Anteriorly, the medial wall of the periotic sac is related to the medial bony wall of the recess; the posterior half, approximately, of the medial wall faces the cranial cavity at the vagus (jugular) foramen. Here the sac is crossed superiorly by a large vein and medially by the vagus nerve. Where it faces the foramen, the medial wall of the periotic sac is not well defined, but appears to be formed by a thin continuation of the lining of the remainder of the sac, backed by loosely organized tissue resembling periotic reticulum; the latter rests medially against a second thin membrane (dural?) which spans the vagus foramen at its internal margin. Although the appearance of this arrangement suggests that the periotic compartment may communicate with that of the cerebrospinal fluid, experimental replacement injections of Evans Blue dye in living anesthetized specimens of *Pseudemys* failed to pass either from the periotic sac into the cerebrospinal fluid, or from cerebrospinal fluid into the periotic spaces. Radiographic examinations of several specimens following perfusion with mercury (method of Young, 1952) further indicated that the periotic sac does not communicate with the cerebrospinal fluid compartment.

Laterally, within the recessus scalae tympani, the periotic sac abuts against the medial wall of the compartment termed by de Burlet (1934) the "pericapsular sinus"; I find this relationship clear in all specimens of the three genera examined. From its blind posterior extremity, which extends to the posterior extremity of the periotic sac, this sinus extends anteriorly to enter the recessus cavi tympani (Romer, 1956) lateral to the periotic foramen and diverges from the periotic sac. Within the recessus cavi tympani and forming its major content, the sinus extends anteriorly adjacent to the lateral wall of the otic capsule. Lateral to the footplate of the columella auris, the lateral surface of which it lies against, the sinus is traversed by the shaft of the columella. Anterior to this, at the level of the anterior margin of the fenestra ovalis (vestibuli), the sinus ends blindly.

In fresh material, this sinus is filled with a clear viscous fluid which is, subjectively, unlike either periotic or cerebrospinal fluid. In fixed and sectioned material, the contents of the sac shrink, fail to occupy the sinus completely and form a homogeneous translucent mass which stains blue with Mallory's technique, or pale green with the Patay-Masson method cited by Gray (1954). Replacement injections of Evans Blue dye made into this sinus fail to enter either the periotic or cerebrospinal fluid, and, conversely, dye in the cerebrospinal or periotic fluid does not color the fluid of the sinus. It is, therefore, apparently a closed compartment and, in this respect, unlike the juxtastapedial sinus of colubrids. Further indication that this structure in turtles is not homologous to the ophidian sinus is found in embryos of *Chrysemys* in which the sinuses of the right and left sides communicate via a canal passing between the basisphenoid and parasphenoid primordia at the level of the external glossopharyngeal foramen. Therefore, believing this sinus to be no more than analogous to the juxtastapedial sinus of ophidians, and rejecting de Burlet's (1934) "pericapsular sinus" on the grounds that the term is misleading, I suggest that it be termed *paracapsular sinus.*

CROCODILIA

Crocodylidae

(Figs. 46-47)

The general organization and histology of the internal ear in *Alligator* are covered in considerable detail by Retzius (1884), but his observations on the periotic channels, although accurate, are incomplete. The periotic system in *Crocodylus* receives special attention from de Burlet (1929, 1934), and his interpretation has been generally accepted as representative of the condition in the crocodylids. Although these authors, particularly the former, mention the relationships between the saccule, cochlear duct and otic capsule, these relationships profoundly influence the organization of periotic channels and differ sufficiently from those in other reptiles to merit brief consideration here.

In both *Alligator* and *Caiman* the saccule is of moderate size, slightly compressed transversely, and has the form of a rounded oval when viewed from its lateral aspect. Situated well medially in the vestibular recess, its thick medial wall is related to the capsular wall inferiorly and to the utricle superiorly; the lateral saccular wall is thin. Posteriorly, the saccule gives rise to a short elliptical ductus reuniens, which hooks inferolaterally to join the cochlear duct.

The latter is composed of two distinct limbs. From the junction with the ductus reuniens lateral to the posteroinferior part of the saccule, the proximal limb of the cochlear duct slopes anteroinferiorly through the vestibular recess to an area just lateral to the posterior acoustic foramen; here a genu is formed and from it the distal limb of the duct extends abruptly inferiorly into the deep, tubular, cochlear recess. The distal limb is slightly longer than the proximal, and houses the lagenar macula in its terminal, slightly expanded, blind end. As pointed out by Retzius (1884), the vestibular membrane ("tegmentum vasculosum") and the limbus ("Knorpelrahmen der Pars Basilaris") spiral subtly and shift their relationships throughout the length of the cochlear duct. In general, however, the vestibular membrane may be said to form the superomedial wall of the proximal limb of the cochlear duct and the anterior wall of the distal limb; the limbus (and contained basilar membrane) form the inferolateral wall of the proximal limb, and the posterior wall of the distal limb.

Situated in the fenestra ovalis, superolateral to the cochlear duct, the footplate of the columella faces inferomedially toward that duct and the posteroinferior part of the saccule. Immediately posteroinferior to the fenestra, the periotic foramen perforates the posterolateral wall of the otic capsule, lateral to the posterior part of the proximal limb of the cochlear duct. The superior margin of the periotic foramen, easily defined, is formed anteriorly by the narrow strut of bone which forms the inferior margin of the fenestra ovalis; the anterior and posterior margins are, likewise, readily identified. The inferior margin is, however, obscured by its intimate relationship to the base of the processus subcapsularis (of de Beer, 1937).

Internal to those openings, the limbus makes attachments which result in a longitudinal division of the vestibular recess and extend to subdivide the cochlear recess. The lateral margin of the limbus attaches to the internal surface of the strut of bone between the fenestra ovalis and periotic foramen; anterior to that strut, the lateral attachment is continued beneath the fenestra ovalis to the posterior margin of the cochlear recess, and, posteriorly, it continues superior to the periotic foramen. Posterior to that opening, the limbic attachment sweeps inferomedially across the posterior wall of the vestibular recess, then turns rostrally along a slight ridge which runs anteriorly to the medial margin of the mouth of the cochlear recess. Both medial and lateral attachments continue into the latter; here the medial attachment is the stronger, but both continue to a level just short of the superior limit of the lagena. Thus, these attachments define one space which lies superomedially in the vestibular recess and extends into the anterior part of the cochlear recess, and a second which reaches from the vicinity of the periotic foramen into the posterior part of the cochlear recess.

The periotic cistern lies in the superomedial of these two cavities. Irregularly triangular in transverse section, the cistern is in contact with the lateral wall of the saccule, and inferolaterally rests against the vestibular membrane of the proximal limb of the cochlear duct. The third, superolateral, wall of the cistern abuts against the lateral wall of the vestibular recess, and, more inferiorly, against the footplate of the columella auris. The latter is so oriented that it faces directly toward the inferomedial part of the cistern. A short saccular part of the cistern extends rostrally into the anterior extremity of the vestibular recess, completing the cisternal contact with the lateral saccular wall. In my material, including late embryos and young specimens of *Alligator* and *Caiman,* I have been unable to find any periotic channel corresponding to the "ductus brevis" described by de Burlet (1929) in *Crocodylus.* Except in sections showing artefacts of fixation or sectioning, the periotic cistern appears to be without any direct communication with the periotic compartment corresponding to that author's "scala tympani."

The scala vestibuli arises from the anteroinferior extremity of the periotic cistern and extends ventrally into the cochlear recess. Situated anterolateral to the distal limb of the cochlear duct, the scala is irregularly crescentic in cross section, and lies in contact with the vestibular membrane and the lateral surface of the limbus of the distal limb. In the depths of the recess, an extension of the scala vestibuli expands anterolaterally into a small bony recess opposite the thin anterolateral wall of the lagena. This extension of the scala abuts against the lagena opposite the lagenar macula and probably corresponds to the scala lagenae of lacertilians.

The helicotrema arises from the scala vestibuli superior to the upper limit of the lagena. It extends medially from the posterolateral part of the scala and, grooving the lateral margin of the limbus, traverses the attachment of that structure to open, posterior to it, into the scala tympani.

At the level where it is entered by the helicotrema, the scala tympani is situated in the posterior cavity of the cochlear recess, bounded medially and laterally by the limbus and its attachments, and in contact with the basilar membrane anteriorly. Just inferior to this level, the medial and lateral parts of the limbus are united by a curved plate of limbic tissue, which is associated with the terminal part of the cochlear duct. An inferior extension of the scala tympani passes anterior to this plate and extends downward between it and the lower extremity of the basilar membrane; the extension terminates blindly at the level of the inferior limit of the basilar papilla. This scalar extension, which can be interpreted as an accessory scala tympani, is described and figured by Retzius (1884).

Attention should be called, however, to the fact that Retzius incorrectly believed a periotic space posterior to the limbic plate at this level to be the scala tympani; this is actually not the case, for my material shows conclusively that the area is closed from the tympanic scala by the firm attachment of the plate to the posterior wall of the cochlear recess immediately inferior to the helicotrema. The terminal part of the limbus and cochlear duct are but loosely attached to the posteromedial wall of the recess, and by some sparse periotic reticulum posteriorly; the space remaining is in lateral communication with the terminal part of the scala vestibuli.

The scala tympani extends superiorly in the cochlear recess, retaining the relationships noted at the level of the helicotrema. At the genu of the cochlear duct and limbus, the scala turns caudad and immediately terminates in the periotic sac. The intracapsular part of the sac is larger than the scala tympani and occupies the space inferolateral to the proximal limb of the cochlear duct. It is in contact with the basilar membrane superomedially. A narrow, short, blind extension of the sac invades the thick posterior part of the limbus to reach the posterior extremity of the basilar membrane. This blind extension, like the one at the distal extremity of the scala tympani, is described and figured by Retzius (1884), and can also be defined as an accessory scala tympani.

Laterally, the periotic sac traverses the periotic foramen and expands into the space delimited by the processus subcapsularis (of de Beer, 1937) and situated lateral to the posteroinferior part of the otic capsule. Anterosuperiorly, at the fenestra pseudorotunda (of de Beer), the extracapsular part of the sac touches and fuses with the mucosa of the tympanic cavity to form the large oval secondary tympanic membrane. Attached medially to the external surface of the strut of bone separating the fenestra ovalis from the periotic foramen, the membrane lies immediately posterolateral to the footplate of the columella auris and faces anterosuperiorly into the tympanic cavity. Posteroinferiorly, the sac bulges medially, enclosed between the processus subcapsularis and the posteroinferior wall of the otic capsule. Extending toward the cranial cavity, this part of the periotic sac lies anterior to the ganglion of the vagus nerve and is in intimate medial association with the glossopharyngeal nerve. The sac itself does not reach the dura mater, but a strand of loose connective tissue resembling periotic reticulum does extend from its medial wall to attach to the dura immediately adjacent to the point of exit of the glossopharyngeal nerve.

DISCUSSION

As represented by the forms included in this investigation, the sacculo-cochlear (inferior) division of the reptilian periotic labyrinth consists of: (1) a variably-divided intracapsular body of periotic fluid interposed between the footplate of the columella auris and the vestibular membrane of the cochlear duct; (2) a narrow curved channel, here termed the helicotrema, which connects the above with (3) a broad channel and/or sac associated with the basilar membrane, the periotic foramen, the glossopharyngeal nerve and remnants of the embryonic metotic fissure; and (4) specialized periotic diverticula associated with the receptor areas of the saccule and cochlear duct. The fluid contained within these channels and compartments extends to fill spaces in the periotic reticulum of the superior division of the otic labyrinth, but does not communicate (unless by way of selectively permeable membranes) with either otic or cerebrospinal fluid compartments.

This general organization of parts of the periotic labyrinth seems entirely compatible with that which might be expected of an ancestral stock derived from an amphibian line and leading eventually to mammals. Accounts by Retzius (1881), Harrison (1902) and de Burlet (1929, 1934) indicate that comparable parts and organization are present in the ear of recent amphibians. A periotic (perilymphatic) cistern is situated between the equivalent of the footplate and the lateral wall of the saccule, and is connected with a medially-placed periotic (perilymphatic) sac by a long narrow helicotrema (perilymphatic duct) which passes in intimate relationship to the lagena. The periotic sac, although specialized in its mode of relationship to the receptor areas, is closed, and lies in an intracapsular and intracranial position immediately anterior to the vagus (jugular) foramen; in *Bombinator* and *Rana* a part of the sac extends externally through the vagus foramen (de Burlet, *ibid.*). Although the periotic systems of these animals show considerable specialization in detail, they could easily be derived from a system similar to that in *Sphenodon*. Romer (1956) postulates an organization of foramina in the medial wall of the otic capsule in primitive amphibians and reptiles (anthracosaurs, *Seymouria* and *Kotlassia*) virtually identical to the arrangement of similar openings in the otic capsule of *Sphenodon*. Extrapolating from these data, it seems reasonable to assume that the basic organization of the periotic labyrinth was established early in amphibian stock, and has remained relatively unchanged, despite the change in vibratory receptors which are believed to have taken place during the evolution of the amphibians.

Aside from questions concerning the homology of the mammalian fenestra rotunda (cochleae), which appear to have been satisfactorily answered by de Beer (1929, 1937), the part to part relationship of the reptilian periotic labyrinth to that of mammals seems to have gone unquestioned in the literature. Referring to the morphology of the ear in crocodylids and birds, de Burlet (1934), Gray (1955) and others point out the simplicity of the cochlear channels in *Echidna* and compare them directly to those of (presumably) a reptilian ancestor. Under the generally-accepted conditions of communication of the periotic system with subarachnoid spaces in mammals (Bast and Anson, 1949; Wolff, Bellucci and Eggston, 1957; standard works on gross human anatomy and the mammalian ear) such a direct transition seems extremely unlikely, if not impossible. As noted above, the periotic sac in amphibians is described as a closed compartment, and the observations of this investigation have consistently indicated that there is no communication between the two compartments in any of the modern reptiles investigated. These observations find support (primarily in figures) in de Burlet's (1929, 1934) treatment of reptiles other than ophidians, and in the work of Shute and Bellairs (1953). It seems improbable that a system isolated from fluid interchange throughout a great part of its prior evolution would suddenly achieve such contact in mammals.

Suggestions that periotic and cerebrospinal fluids are not in communication in mammals do appear in the literature. Streeter's (1918) study of the development of the periotic spaces fails to show their communication with subarachnoid spaces, and the work of Waltner (1948) casts further doubt concerning the existence of such a communication. Young (1952 and personal communication) presents convincing evidence that the periotic (perilymphatic) duct in some mammals terminates in a small blind sac situated adjacent to the meninges in the jugular fossa. Using Young's procedure, I have been able to duplicate his results in human temporal bones, and in cats, dogs and rabbits. Experimental replacement injections of Evans Blue dye into the cysterna magna and vestibule in rabbits further indicate that the periotic system is not in free communication with the cerebrospinal fluid. This situation is that which might logically be expected if one assumes direct homology of the mammalian system with that of reptiles.

As suggested above, the periotic labyrinth of *Sphenodon* is considered to be the most primitive of those treated in this investigation, and might well be similar to that of some of the earliest known reptiles. Price (1935) and Romer (1956) point out the unossified condition of a part of the medial wall of the otic capsule in *Captorhinus,* an area similar to one in seymouriamorphs in which the latter author postulates a periotic foramen. Such placement, similar to that in *Sphenodon,* would allow for either an intracranial periotic sac such as is found in some amphibians, or for extension of such a sac through the adjacent large vagus foramen. Romer, in fact, states that such an extension may have accompanied the glossopharyngeal and vagus nerves in *Captorhinus.* Assuming this condition to have existed, the extension of the periotic sac almost certainly ended blindly in the suprapharyngeal region, since the external orifice of the vagus foramen in this and other primitive reptiles is placed in a position incompatible with the formation of a secondary tympanic membrane.

Some additional support may be inferred from the contents of the otic capsule. The periotic labyrinth of *Sphenodon* shows little specialization, bears a reasonable resemblance to that of modern amphibians, and would require the postulation of only a few changes for the derivation of the systems noted in the other reptiles investigated. The medial origin of the ductus reuniens from the saccule is more reminiscent of the conditions described in amphibians than it is of the posterior or posteromedial placement found in other reptiles. Furthermore, the size of the basilar papilla in relation to the size of the lagenar and saccular maculae is less in *Sphenodon* than in other reptiles included in this study or recorded in the figures of Retzius (1884). Weston (1939) infers that this fact is indicative of the primative nature of the auditory apparatus of *Sphenodon.*

Changes in the periotic labyrinth from the presumed primitive organization appear to be associated with alterations in the otic capsule and adjacent parts of the skull, modifications in size, position and attachments of the parts of the inferior division of the otic labyrinth, and changes in the size of the basilar papilla and lagenar and saccular maculae. Three major lines of evolution seem to be represented by forms considered in this investigation and correspond to the usual taxonomic grouping of the Squamata, Chelonia and Crocodilia. As noted below, the ophidians might be considered as forming a fourth line, as is implied by de Burlet (1934), but probably may be more properly considered as showing no more than a strong modification of the lacertilian pattern.

The most obvious "advance" shown by lacertilians is the formation of a secondary tympanic membrane. This is associated with a slightly more caudal placement of the periotic foramen than that shown by *Sphenodon*, and varying degrees of division of the metotic fissure into the definitive recessus scalae tympani and vagus foramen of the adult. In all lacertilians examined the periotic sac traverses the periotic foramen to enter the recess and form the secondary tympanic membrane within its confines. In most of the forms examined, the membrane is attached near the margins of the recess and faces directly into the tympanic cavity forming part of its medial wall. In the representatives of gekkonoid families and in *Cnemidophorus* (Teiidae), however, the periotic sac occupies only the superomedial part of the recess, and the secondary tympanic membrane faces inferiorly or inferolaterally into a deep pit in the medial tympanic wall formed by the unoccupied part of the recess. A similar situation is reported in *Ctenosaura* (Oelrich, 1956), and the condition in *Anolis* approaches this, but it was not found to be pronounced in any other iguanids considered here.

This variable location of the secondary tympanic membrane leads to an unfortunate confusion in the meaning of the term "recessus scalae tympani" when it is applied in lacertilians. In his definition of the space, de Beer (1937:431) states:

> "In all Tetrapod vertebrates a diverticulum of the perilymphatic spaces of the ear emerges through the foramen perilymphaticum in the wall of the auditory capsule, and finds itself in an extracranial and extracapsular space, the recessus scalae tympani, situated in the anterior region of the fissura metotica. The recessus scalae tympani communicates with the cranial cavity through its apertura medialis which coincides with the anterior portion of the fissura metotica, and over its apertura lateralis is stretched the secondary tympanic membrane, which separates the recessus scalae tympani from the tympanic cavity."

Not only does this definition present problems (noted below) when applied in lacertilians in which the secondary tympanic membrane is deeply placed, but it also seems inapplicable either in forms lacking a true secondary tympanic membrane or in those in which the periotic sac terminates in, or traverses, the cranial cavity (amphibians; *Sphenodon*). Employing a more common, less restrictive interpretation, Romer (1956:118) says of the area in lizards, the only group in which he applies the term regularly:

> "Anteroventral to the vagus foramen is the recessus scalae tympani, formed from the lower part of the embryological metotic fissure. The perilymphatic duct enters this recess from the ear capsule, sends one branch inward to the brain cavity and a second outward to a membrane facing the middle-ear cavity;

the structure is thus comparable to (but not strictly homologous with) the mammalian fenestra rotunda."

These two definitions, the former based upon the position of the secondary tympanic membrane and the latter applied to a bony cavity, are compatible only when the periotic sac completely fills the cavity.

In his description of *Ctenosaura,* Oelrich (1956:17) solves the problem of the deeply-placed membrane as follows:

> "Medial to the crista interfenestralis is a deep occipital recess, bounded posteriorly by the crista tuberalis (Säve-Söderbaugh, 1945, 1947) and ventrally by a similar recess in the basioccipital. In the occipital recess, near its apex, lies the foramen rotundum, marked by a small crest and covered by the membrana tympani secunda. Beyond this foramen in the cavity of the exoccipital is the small triangular recessus scala tympani, whose medial wall is the foramen perilymphaticus (Fig. 9), which opens into the cranial cavity, and on whose superior wall is the fenestra cochlea (Fig. 12), which opens into the medial surface of the lagenar recess. The recessus houses the terminal end of the saccus perilymphaticus and transmits the glossopharyngeal nerve."

Disregarding divergences in the application of some terms, this approach conforms to de Beer's (1937) definition, but necessitates the introduction of the term "occipital recess" for the designation of the part of the fossa external to the secondary tympanic membrane. This does not seem desirable, since in this system the terms "occipital recess" and "recessus scalae tympani" designate different regions of a fossa which has commonly been recognized by the one (latter) name.

It seems that a satisfactory solution might be found for all forms in which a recessus scalae tympani exists by defining the space as—an extracranial and extracapsular fossa, derived from the anteroventral part of the metotic fissure, which communicates with the cranial cavity by way of a medial aperture and with the otic capsule by way of the periotic foramen, and which contains part or all of the periotic sac. Deliberately general, such a definition does not seem to conflict with the usage of the term in osteological literature, and allows sufficient flexibility for its application in forms in which the space is enclosed or unrelated to a true secondary tympanic membrane.

The relatively limited sampling precludes firm evaluation of the significance of deep placement of the secondary tympanic membrane within the recessus scalae tympani, but several items seem worthy of note. The geckos, in which the feature seems to be consistent, are commonly considered to be members of an archaic group (Shute and Bellairs, 1953; Romer, 1956), and Smith (1946) considers *Ctenosaura,* in which Oelrich (1956) reports a deeply placed membrane, to be a primitive iguanid. According to Romer (*ibid.*) the teiids are a "relatively primitive family" of leptoglossans, a group which he regards as being "a 'higher' lizard assemblage." Shute and Bellairs (*ibid.*), however, point out similarities in the structure of the internal ear in *Tubinambis* to that in geckos; their observations find support, although less striking than that which they indicate, in a comparison of the teiid *Cnemidophorus* with the geckos considered here. Taken together, these things suggest that deep placement of the secondary tympanic membrane may be a relatively primitive lacertilian feature. Subjectively this is borne out, since deep placement of the membrane is associated with a medial or posteromedial placement of the periotic foramen, one which is more like that in *Sphenodon* than like the posteroventral or posterolateral placement noted in forms in which the secondary tympanic membrane is situated in the plane of the medial wall of the tympanic cavity. Furthermore, the association of the periotic sac with the dura mater tends to be intimate in forms with the membrane deep in the recessus scalae tympani; as noted above, the sac actually bulges into the cranial cavity in *Cnemidophorus.* These features could be interpreted as representing an intermediate stage between the presumed primitive, sphenodontid, condition and the relationships common in those forms in which the periotic sac fully occupies the recessus scalae tympani.

A second line of specialization in the lacertilian periotic labyrinth is indicated in the variable division of the periotic cistern which results in the formation of a scala vestibuli; this is usually accomplished by a cisternal septum and/or bony ridge marking the superior lateral margin of the cochlear recess. Some indication of development of these structures, with the resultant definition of a scala vestibuli, is found in all families of lizards investigated. Least marked in *Cnemidophorus* and *Ophisaurus,* in which only a short indistinct ridge is present, the separation shows varying degrees of completeness culminating in the situation noted in *Aristelliger,* in which the separation of the scala vestibuli from the saccular part of the periotic cistern is complete except for a narrow communication between the two in the posterior extremity of the otic capsule. Like the deeply-placed secondary tympanic membrane, the cisternal septum does not appear to be a feature which shows any continuous graded development throughout the lizards as a whole, but rather appears to have been developed progressively, and in a parallel fashion, in different groups. For example, the iguanids *Crotaphytus, Sceloporus* and *Uta* show absence or weak development of the septum, while in *Phrynosoma* and *Anolis* the structure is marked, but shows differences in its degree of development and relationship to the fenestra ovalis. In gekkonoids examined the septum and ridge are consistently present but show variable degrees of development. In *Coleonyx,* the arrangement is similar to that in *Anolis* in that the division is anterior to the fenestra ovalis, but the ridge to which the septum attaches is more strongly developed than in iguanids. *Sphaerodactylus* has both septum and ridge anterior to the fenestra, but continues the ridge posteriorly for the full length of the cochlear recess. *Hemidactylus* and *Aristelliger* both have a complete ridge; in the former a cisternal septum is present and extends above the fenestra ovalis to a level caudal to the midpoint of that opening, while in the latter, direct attachment of saccular periotic tissue accomplishes the division of the periotic cistern to a level caudal to the fenestra ovalis. It should be pointed out that, although the position of the septum and ridge in gekkonoids is similar to that in other lizards, the contribution of bone to the division is greater than in other forms. Poorly marked division of the periotic cistern in *Cnemidophorus* and *Ophisaurus* coupled with the presence of a scala vestibuli in scincids, lacertids and varanids suggests that a progressive separation of the scala vestibuli from the periotic cistern may also have occurred in leptoglossans and diploglossans, but the material available does not warrant a positive statement on this point.

Generally speaking, the extent of development of the cisternal septum, or direct attachment of the saccule to the wall of the otic capsule, can be more directly correlated with the size and position of the cochlear receptors than it can with the function of fixation of the saccule and cochlear duct. Although the latter function is undoubtedly present, it appears to be secondary to that of delimitation of a scala vestibuli. Iguanids suggest this, for the basilar papilla is more strongly developed in *Anolis* and *Phrynosoma* than in other forms, and in these the cisternal septum is well developed. More convincing is the organization in the gekkonoids; in *Coleonyx* and *Sphaerodactylus,* in which the degree of development of the basilar papilla is less than that in the gekkonids, the septum is present only anterior to the fenestra ovalis. On the other hand, in *Aristelliger* and *Hemidactylus* in which the basilar papilla is enlarged by extending posteriorly, the scala vestibuli can be defined in relationship to the entire lateral wall of the cochlear duct. In scincids, elongation of the basilar papilla approaches that noted in geckos, but the receptor develops anteriorly rather than posteriorly. The scala vestibuli is present only anterior to the fenestra ovalis in the forms examined, but this position places it opposite the anterior part of the receptor. Thus, position of the receptor seems to be an important correlate to the degree of scalar development. It seems, therefore, that the differentiation of a scala vestibuli, either by a cisternal septum or by direct attachment of the saccule to the lateral wall of the vestibular recess, is associated with restriction or "channeling" of vibrations introduced by the footplate to the lateral wall of the cochlear duct opposite the basilar papilla and lagenar macula. Its structure and position in lizards seem entirely compatible with such a function.

The scala lagenae, prominent in *Sphenodon,* is reduced in all lacertilians examined. In iguanids, as noted earlier, the development of the channel correlates well with the size of the lagenar macula; this holds true, because in the specimens examined the scala lagenae constitutes the major periotic association of the lagenar macula. This association does not appear to be consistent through all groups of lizards; in the gekkonoids, for example, the lagenar macula lies opposite a scala lagenae, but is also associated with the scala vestibuli and the helicotrema. Generally speaking, the scala lagenae appears to be relatively consistent within families of lizards; in higher taxonomic assemblages, its development varies with the position of the lagenar macula in relation to the scala vestibuli or periotic cistern, as well as with the size of the receptor. Seemingly, the only generalization possible, concerning the structure in lacertilians as a whole, is that it is well developed in those forms in which the lagenar macula is large and distinctly ventral to the plane of the basilar papilla, and reduced in those forms in which the receptor is higher or smaller. Its sole function appears to be to extend the periotic cistern or scala vestibuli sufficiently to bring lateral periotic fluid channels into relationship with that part of the cochlear duct housing the macula lagenae. This is in itself interesting, however, for de Burlet (1929, 1934) states rather strongly that periotic channels are not related to the lagena, but are blocked from such association by periotic reticulum (his "Bindegewebsbalken").

The periotic channel here termed the scala sacculi was noted in eublepharids, gekkonids, lacertids, anguids and varanids. Although variable in its anterior and posterior communications, the channel is consistently related to the inferior part of the medial wall of the saccule and in communication inferolaterally with the scala vestibuli or corresponding part of the periotic cistern. These relationships are extremely similar to those of the inferomedial part of the periotic cistern (that part situated between the medial wall of the saccule and opposing lateral wall of the cochlear duct) of *Sphenodon.* A marked resemblance of the scala to the sphenodontid structure is present in *Varanus,* in which the ductus reuniens originates from the inferomedial wall of the saccule and continues into a cochlear duct extending significantly more ventrally than anteriorly. Other forms show varying decreases in the freedom with which the channel communicates with the periotic cistern anterior and posterior to the saccule, and reduction in the size of the lateral communication with the scala vestibuli or periotic cistern. The degree of isolation shown by the saccular scala correlates well with the relationship between the saccule and cochlear duct; those forms in which the ductus reuniens originates more medially from the saccule and extends into a ventrally-directed cochlear duct show freer communications than those forms in which the ductus reuniens criginates posteriorly from the saccule and the cochlear duct extends anteriorly beneath it. These things seem to indicate that the scala sacculi may well be derived from the inferomedial part of a primitive periotic cistern similar to that in *Sphendon.* Its formation has probably been associated with the shifting of the origin of the ductus reuniens from the medial to the posterior surface of the saccule, and assumption by the cochlear duct of a position adjacent to the inferior margin of the saccule.

It is noteworthy that the scala sacculi is most clearly defined and isolated from communication with the superior part of the periotic cistern in *Hemidactylus, Coleonyx* and *Lacerta*; in these forms, the scala extends as a clear channel only from the scala vestibuli to the base of the saccular macula. In *Coleonyx,* the central part of the lateral wall of the saccule is thick, and in *Hemidactylus,* the entire lateral wall is thickened and attached to the wall of the vestibular recess. In *Lacerta,* the lateral wall of the saccule is not structurally modified but does contact the lateral vestibular wall, excluding the periotic cistern from its typical contact with that part. These modifications, all resulting in alteration of the usual relationship of the periotic cistern, coupled with the intimate association of the saccular scala with the base of the macula sacculi, suggest that the scala may, in these forms at least, serve as a conducting channel for vibratory stimuli. Such a conclusion seems quite reasonable since the works of von Frisch (1938) and Weston (1939) support interpretation of the saccular macula as a vibratory receptor (in part) in lower vertebrates. In his consideration of the structure, de Burlet (1929, 1934) questions its function and tentatively assigns it to both the equilibratory and auditory systems, largely on the grounds of the consistent association of the periotic cistern with the lateral wall of the saccule. Thus, although it is probably derived from a primitive periotic space and may, in some forms, be indicative of a primitive organization in the ear, the scala sacculi appears to form a highly specialized vibratory conducting channel in some lizards.

It is quite apparent that the periotic cistern and its derivatives are intimately linked ontogenetically (and probably phylogenetically) with the morphology of the saccule and cochlear duct, and with the size, shape and location of the three receptors they contain. Subjective observations made in connection with this study indicate that investigation of the general morphology of these structures, coupled with a detailed analysis of their receptors might yield valuable otological and taxonomic information.

The helicotrema in lacertilians is extremely consistent in its form and relationships; particularly stable are its relationships to the anterior extremity of the cochlear duct and to the posterior acoustic foramen. The degree to which it grooves the wall of the cochlear recess is variable and ranges from slight grooving of the anterior wall to the formation of a bony canal in the anterior wall of the cochlear recess. The latter condition was noted only in *Coleonyx* and *Sphaerodactylus;* the gekkonids examined showed only grooving comparable to that found in most other lizards.

The recognition of both a scala tympani and periotic sac may be questioned, since not only do the scala and intracapsular part of the sac form a morphological and functional continuum, but the works of de Beer (1929, 1937) rather clearly indicate that at least the intracapsular part of the sac is represented by part of the scala tympani in mammals. On the other hand, that part termed scala tympani is clearly differentiated from the intracapsular part of the periotic sac in lacertilians, and the latter can be only arbitrarily separated from the extracapsular part of the periotic sac; therefore, the recognition of both scala tympani and periotic sac in lacertilians seems justified on morphologic grounds.

The scala tympani and intracapsular part of the periotic sac show considerable uniformity in their relationships throughout the lacertilians examined. Occupying the space between the limbus and basilar membrane laterally, and the wall of the cochlear recess and its periotic foramen, the channels do vary in size and shape in different forms. Differences noted seem to depend not only upon the attachments of the limbus and its relationship to the periotic foramen, but, particularly, upon the shape and degree of development of the basilar papilla and membrane. In most forms, variations in the form and relationships of cochlear structures may be considered minor, and are accompanied by minor changes in the form and size of the periotic sac. In eublepharids, gekkonids, varanids and scincids, however, the basilar papilla and membrane are elongate and are related to a special diverticulum of the periotic sac, here termed the accessory scala tympani. Shute and Bellairs (1953) report the presence of such diverticula in geckos, and Retzius (1884) records them in several skinks; the diverticulum has not been previously reported in varanids. Obviously a specialization to allow intimate relation of periotic fluid to the elongated basilar papilla and membrane of these forms, the accessory scala tympani extends from the intracapsular part of the periotic sac, traverse a groove in the lateral surface of the limbus and ends blindly at the limit of the basilar membrane. In scincids, the accessory scala extends rostrally from the anterior surface of the periotic sac and is situated ventral to the scala tympani and medial limb of the helicotrema; in the other families in which it is present, the accessory scala reaches posterosuperiorly, and is undoubtedly analagous to the scincid channel. In *Varanus,* the accessory scala is aligned with the scala tympani and arises from the small intracapsular part of the periotic sac, while in representatives of the two gekkonoid families in which it was observed, the accessory scala arises from a large periotic compartment and forms a distinct angle with the scala tympani and medial limb of the helicotrema; aside from these differences, the structures are quite similar. Lacking information on the development of the accessory scala tympani in these families, one may conservatively assume that the varanid channel represents a modification of the periotic sac paralleling that in the two gekkonoid families.

Ophidians show relatively little modification of the intracapsular part of the periotic labyrinth. The periotic cistern, scala vestibuli and cisternal septum have relationships to the saccule and cochlear duct essentially like those in lacertilians in which the cochlear duct parallels the inferior margin of the saccule. The lateral relationships of these structures are, however, considerably altered by the relatively great size of the footplate of the columella auris. Constituting a major part of the inferolateral wall of the otic capsule, the superior half of the elongated footplate faces into the vestibular recess, and the inferior half looks into the cochlear recess; the longitudinal midline of the footplate thus occupies a position equivalent to the position of the ridge marking the superior lateral margin of the cochlear recess in lacertilians. Extending laterally, the cisternal septum attaches to the internal periosteum of the footplate. The size of the footplate, coupled with its relationships to the cisternal septum and structures of the otic labyrinth lend attraction to ideas of capsular origin of the columella auris such as Möller's (1905), but evidence presented by de Beer (1937) against such an interpretation makes it seem more reasonable to assume that the relationship of the septum to the footplate has been otherwise acquired. The limited sampling of ophidians suggests that a cisternal septum may have been present in their ancestral stock, but the progressive development of the septum in different groups of lacertilians makes equally possible the assumption that snakes have developed the septum independently and that it has extended its attachment posteriorly onto the footplate.

The helicotrema and medial periotic channels show relationships identical to those in lacertilians, but the periotic sac is considerably reduced in size and appears attentuated as a result of the posterior placement of the periotic foramen. The slight enlargement of the scala tympani adjacent to the basilar membrane doubtless represents the intracapsular part of the sac, and communicates directly with the sacciform enlargement occupying the recessus scalae tympani; recognition of the homology by direct application of the terms used in lacertilians does not, however, seem desirable.

As recorded by de Burlet (1934), it is in the extracapsular part of the periotic system that ophidians diverge markedly from lacertilians. That author terms the entire extracapsular compartment the "pericapsular sinus" and reports a direct communication of this compartment with cerebrospinal fluid spaces (submeningealen Raum); although he is not explicit concerning the location of this communication, his figures indicate that it must occur through the opening recognized above as the medial aperture of the recessus scalae tympani. Apparently the fragile membranes covering the medial aperture of the recess in his material were destroyed in preparation, as frequently happens; lacking this, identification of the periotic sac within the recess is difficult, and one might logically reach conclusions such as de Burlet's. Actually, the relationships of the periotic sac at the medial aperture of the recess are identical to those found in most lacertilians; de Beer (1937) reports similar findings, but notes minor variations in the relationship of the glossopharyngeal nerve to the sac and medial aperture of the recess. Such consistency in these relationships suggests that ancestral ophidians must have been derived from a stock in which the periotic sac occupied part of a definitive recessus scalae tympani, rather than from a more primitive one in which the periotic sac presumably traversed the cranial cavity and vagus foramen; only lacertilians show a directly comparable series of relationships.

The radical alteration of the lateral relationships of the periotic sac seems to be, in large part, attributable to the encroachment of the opisthotic upon the area of the lateral aperture of the recessus scalae tympani in the formation of the posterior part of the circumfenestral crest. Extending anteroventrally, the process crosses the usual lateral aperture and leaves two foramina. One of these looks posteriorly into the vagus foramen, is traversed by the glossopharngeal nerve and can only be interpreted as representing the posterior part of the lacertilian lateral aperture. The anterior part of the lateral aperture is thus represented by the foramen situated posteroventral to the footplate of the columella auris and forms the communication between the recessus scalae tympani and the juxtastapedial fossa. Thus, the juxtastapedial sinus is actually an extension of the periotic sac outside the confines of the recessus scalae tympani, and occurs only in ophidians. The membrane formed at the mouth of the juxtastapedial fossa must, therefore, be analogous to the secondary tympanic membrane of lizards rather than homologous, as is suggested by de Beer (1937).

The suggestion is advanced by de Burlet (1934) that this arrangement probably constitutes a dampening mechanism, but he does not speculate concerning its mode of action. It is possible that the membrane may allow some dampening of vibrations in the periotic fluid against the mandibular musculature (and this concept finds indirect support in *Carphophis* in which the size of the membrane is reduced and the area of contact of the periotic sac with the dura at the medial aperture of the recessus scalae tympani is correspondingly enlarged), but it seems that the primary significance of this arrangement is that it allows a reciprocating movement of the columella auris and periotic fluid. Thus, inward movement of the footplate displaces periotic fluid, but at the same time provides for accommodation of displaced fluid by increasing the depth of the juxtastapedial fossa and sinus.

There is some evidence suggesting that the juxtastapedial sinus and fossa may undergo specialization in forms adapted to burrowing. Of the colubrids examined, *Carphophis* shows external characteristics more like those of true burrowing snakes than do the other forms, and I have observed some burrowing behavior in *Carphophis* in the field; the latter is not true of the other colubrids utilized in this investigation. The reduced size of the mouth of the juxtastapedial fossa in relation to the size of the footplate in a form showing these characteristics led to an attempt to ascertain the relationships in true burrowers. Examination of a skull of *Leptotyphlops* showed certain external similarities of the otic region in this form to that of *Typhlops*, as described by Haas (1930). Dissection of the area revealed that the shaft of the columella auris traverses a small opening similar to that designated as the fenestra ovalis in *Typhlops*, and extends internally across a small space before terminating in a distinctly enlarged footplate. A small foramen posteroinferior to the footplate was found to communicate with the cranial cavity. These relationships suggest that the circumfenestral crest has been elaborated in this form and has completely enclosed the juxtastapedial fossa and sinus, except for the small opening traversed by the shaft of the columella. The fossa and sinus would then be intracapsular in the sense that they are completely surrounded by laminae of the prootic and opisthotic, but would retain the same relationships to the footplate as those noted in colubrids. The external opening in the otic capsule of *Leptotyphlops* would, therefore, not be the fenestra ovalis, but the constricted mouth of the juxtastapedial fossa; Haas' (1930) description of *Typhlops* allows speculation that the same relationships may exist in that form. The functional implications of this situation are interesting since closure of the juxtastapedial fossa would result in total dependence upon the reciprocal type of fluid movement suggested above, plus the possibility of some dampening at the medial aperture of the recessus scalae tympani. Sections of complete heads of *Typhlops* and *Leptotyphlops* are now being prepared for study of the precise relationships of the fluid labyrinths.

Chelonians show major divergences in the organization of both the intracapsular and extracapsular parts of the periotic labyrinth. Primarily associated with the accentuated ventromedial direction of the cochlear duct, the periotic cistern, cisternal septum and scala vestibuli have almost vertical rather than horizontal relationships to the footplate of the columella auris. Thus, the periotic cistern is impinged upon by the anterior and superior parts of the footplate, while the scala vestibuli rests against the posterior part of the same structure.

The cribrate lamina designated cisternal septum shows obvious differences in structure from the condensed lamina given the same name in lizards and snakes. Although it finds its medial attachment in the periotic reticulum between the saccule and cochlear duct and extends laterally to separate the cochlear from the vestibular recess, the septum is composed of rather loosely organized tissue bearing little resemblance to that noted in other forms. Furthermore, its continuity anteriorly with ventral saccular attachments finds no direct comparison in the Squamata. Its structure would allow the septum to function in the capacity of disrupting patterns of movement in the periotic fluid, but its relationship to the footplate of the columella auris is hardly compatible with such a function, or with that of fixation of the saccule and cochlear duct. Its intrinsic structure suggests that the cisternal septum is developed independently in chelonians, but the limited sampling precludes positivism concerning this point, and sheds little light on the structural or functional significance of the membrane.

The origin of the helicotrema is related to the cochlear duct in a manner similar to that noted in Rhynchocephalia and Squamata, and the relationships of the terminal part of the channel to the posterior acoustic foramen, to the cochlear ganglion and its branches, and to the limbus are similar to those found in representatives of the groups named. The intermediate part, on the other hand, diverges from the cochlear duct and shows a unique relationship to the medial wall of the saccule in its course toward the posterior acoustic foramen. It is interesting to note that an anteroventral "overgrowth" of the saccule, which penetrated between the helicotrema and anterior wall of the otic capsule in a form having a primitive labyrinthine organization, would produce changes in the helicotrema such as those noted; it would also produce altered relationships of the saccule, cochlear duct and lateral periotic structures to the lateral wall of the otic capsule. It seems reasonable to assume that such a development may have taken place early in the chelonian line, and resulted in the apparent rotation of intracapsular structures seen in modern turtles. Such an assumption seems entirely compatible with the mode of development and definitive structure of the otic capsule as described by de Beer (1937).

As in ophidians, the chelonian scala tympani is undoubtedly homologous to the scala of lacertilians, plus part of the periotic sac. The origin of the channel shows relationships identical to those in Squamata, and the vertical expansion adjacent to the basilar membrane represents the intracapsular part of the periotic sac as it is seen in lacertilians. That part of the scala tympani posterior to the cochlear duct seems to represent that which, in lacertilians, would be the proximal (capsular) extremity of the extracapsular part of the periotic sac. This is borne out by the intracapsular relationship of the glossopharyngeal nerve to the scala, and finds support in the development of the posterior part of the capsule; de Beer (1937) points out that the internal and external glossopharyngeal foramina represent the medial and lateral apertures of the recessus scalae tympani, and indicates that the anterior extremity of the metotic fissure is incorporated into the otic capsule. The chelonian periotic sac is, therefore, the equivalent of only the posterior extremity of the extracapsular part of the rhynchocephalian or lacertilian periotic sac. Although the arrangement of the scala and periotic sac can be derived from a lacertilian type of organization, relationships to the vagus foramen and contained structures suggest that it probably arose by modification of parts little advanced from the presumed primitive organization resembling that in *Sphenodon.*

The paracapsular sinus (pericapsular sinus of de Burlet, 1934) shows consistent morphology in the forms included in this study, and is apparently like that which de Burlet (ibid.) describes in *Testudo;* no indication of an elaborate organization such as that author attributes to *Emys* is present, either in these forms or in the one late embryo of *Emys* I have examined. It seems clear that, as de Burlet suggests, the structure must function as a dampening or release mechanism for movements of the periotic fluid, and would thus be analogous to the juxtastapedial sinus of ophidians. On the other hand, the origin or derivation of the structure is enigmatic. Based solely upon the structure in adult animals, the paracapsular sinus could be derived by postulating extension of the periotic sac into relationship with the footplate (and cranial cavity, if the situation is as de Burlet describes it in adults of *Emys*), with a secondary separation of the extension from the parent cavity. This explanation finds no support in the development of the compartment in embryos of *Chrysemys*, for the periotic sac and paracapsular sinus appear independently and remain so in late (32mm.) embryos. A second possibility is that the paracapsular sinus may actually represent an isolated and highly modified superomedial part of the lining of the tympanic cavity of an ancestral form. As noted above, the paracapsular sinus occupies a major part of the recessus cavi tympani, an area occupied by the tympanic cavity in most reptiles (Romer, 1956). The relationships of the sinus to the facial nerve and internal carotid artery seem to be compatible with such a suggestion, when viewed in the light of the osteological modifications which have occurred in the region. An additional feature of interest is the transverse communication between the right and left paracapsular sinuses noted in embryos of *Chrysemys*. The position of this communication is reminiscent of that of the intertympanic canals of crocodilians (van Beneden, 1882) and at least some mesosuchians (Edinger, 1938). I have found no reference to this channel in the literature, but Nick (1912) shows suggestions of its presence in several of his figures. Its developmental relationships to the pharyngeotympanic tube are not completely clear in the embryonic material available to me, but there is no doubt that both are, morphologically, intimately associated with the paracapsular sinus. Taken together, these items tend to support derivation of the sinus from a part of the lining of the tympanic cavity, but such a conclusion must be considered tentative until more detailed information concerning the development of the tympanic region in turtles is available.

Crocodilians, like chelonians, show major labyrinthine changes indicative of a long independent history. The most significant intracapsular changes influencing periotic channels are the altered positional relationships of the cochlear duct and the relatively tremendous elaboration of that structure. The lateral shift of the cochlear duct results in modified form of the periotic cistern, but its relationships to the lateral wall of the saccule and to the vestibular membrane are retained and the footplate of the columella auris impinges upon the periotic cistern opposite these surfaces. This differs from the situation de Burlet (1929) reports in *Crocodylus*, for he suggests that the footplate is directed only toward the vestibular membrane, and that the saccular part of the cistern is probably not significantly influenced by impulses introduced by the footplate.

The scala vestibuli, although elongated, extends along the distal part of the cochlear duct in relationship to the vestibular membrane and gives rise to a scala lagenae at its distal extremity; there seems to be no reason to question the direct homology of these channels to those given the same name in other reptiles. Conversely, the homology of the crocodilian helicotrema with that in other reptiles is open to question.

In all other reptiles examined, or adequately reported in the literature, the helicotrema is quite consistent in several features of its course and relationships. It turns medially around the anterosuperior surface of the rostral extremity of the cochlear duct and passes medial to the lagenar and cochlear ramuli extending from the cochlear ganglion; furthermore, its relationship to the medial wall of the otic capsule inferior to the posterior acoustic foramen is inflexible. This course and relationships would be duplicated in crocodilians by a channel which arose from the medial aspect of the distal extremity of the scala vestibuli, entered the periotic tissue between the limbus and medial wall of the cochlear recess, and coursed proximally to terminate in the scala tympani opposite the posterior acoustic foramen posterior to the genu of the cochlear duct. The crocodilian helicotrema does not follow such a course, but passes directly from the scala vestibuli to the scala tympani around the lateral margin of the cochlear duct; this relationship would find its equivalent in a helicotrema which passed ventral to the cochlear duct in lacertilians. It is conceivable that this type of association is the result of a fundamental change in the relationships between the helicotrema and cochlear duct, but this seems unlikely in view of the consistency mentioned above. A second possibility, attractive because of its simplicity, would be that an adventitious communication between the two limbs of the helicotrema replaces the normal channel; such a process may have occurred, but it is probably more complex than indicated here.

Retzius (1884) describes and figures periotic spaces in the periotic tissue attaching the limbus to the medial wall of the cochlear recess. These spaces are clear in my material; in young specimens of *Alligator* and *Caiman*, they appear as a series of discontinuous small compartments irregularly aligned along the course postulated for a typical reptilian helicotrema. In late embryos of the same forms, the spaces are relatively larger and show more continuity than they do in older specimens, and in these embryos the helicotrema could not be clearly defined at the lateral margin of the limbus. Taken together, these items suggest that the series of periotic spaces in the medial limbic attachment represents remnants of a typical reptilian helicotrema. It follows that the definitive crocodilian helicotrema is, indeed, a secondary development, but could not have made communication with any part of the medial limb of the original helicotrema. It also indicates that the scala tympani of the distal limb of the cochlear duct is not the direct homolog of the scala tympani of other reptiles, a fact that finds additional support in the manner in which the scala is "embraced" by the limbus. The presence of a definitive accessory scala tympani at the distal extremity of the basilar membrane suggests an explanation for the derivation of the scala tympani and for the crocodilian helicotrema as well.

Accepting the periotic spaces medial to the limbus as representative of the primitive channel (heliocotrema) connecting the scala vestibuli with the periotic sac, contact of the periotic fluid with the basilar membrane of the distal limb of the cochlear duct must have been maintained by means of an accessory scala tympani which traversed the central part of the limbus. With extensive development, such a channel would have been separated from the lateral margin of the scala vestibuli by the more delicate of the limbic attachments, one which is less firm distally than proximally. Under these circumstances, an adventitious communication of the scala vestibuli with the distal part of the accessory scala tympani might easily have occurred at the lateral limbic attachment. Thus, the crocodilian scala tympani distal to the genu of the cochlear duct probably represents the greater part of a highly developed accessory scala tympani, only the tip of which remains recognizable as an entity.

The intracapsular part of the periotic sac requires special comment only in the sense that the part of the periotic system so designated has usually been included as part of the scala tympani (Retzius, 1884; de Burlet, 1929, 1934; and others). Although such nomenclature is undoubtedly justified on the basis of homology of the structure, the size of the channel plus its relationship to the periotic foramen differentiate it morphologically from the remainder of the scala tympani; it seems desirable to recognize this difference, together with the basic similarity in the relationships of the compartment to those in lacertilians, by the use of the term periotic sac. The latter term also serves to differentiate this part of the channel from the two accessory scalae and the derived scala tympani.

Retzius (1884) rather clearly describes the exit of the periotic sac (his "scala tympani") from the otic capsule by way of the periotic foramen (his "foramen recessus scalae tympani") in *Alligator*. It is clear from his description that he regards the space occupied by the extracapsular part of the periotic sac as the recessus scalae tympani. This is supported by de Beer's (1937) osteological analysis of *Crocodylus*, for he describes bony relationships similar to those found in *Alligator* and *Caiman,* and elucidates the manner in which the processus subcapsularis extends the recessus scalae tympani laterally to form the fenestra pseudorotunda. A confusing note is introduced by de Beer (1937:263), however, for he states:

> "The ductus perilymphaticus does not pass through the foramen perilymphaticum (de Burlet, 1929), and thus the 'recessus scalae tympani' in the crocodile fails to contain the scala tympani of the perilymphatic space. The restricted apertura lateralis of the 'recessus scalae tympani,' enclosed between the processus subcapsularis and the wall of the auditory capsule, and across which the secondary tympanic membrane is stretched, bears analogy (but *not* homology) to the mammalian fenestra rotunda, and may therefore in the crocodile be known as the fenestra pseudorotunda."

The apparent conflicts in these statements may be the result of confusion in terminology, but de Burlet (1929, 1934) does imply that the terminal part of the periotic system bears no relationship to the recessus scalae tympani, and de Beer fails to clarify the matter.

In both *Alligator* and *Caiman,* (and presumably in crocodiles since the bony relationships are so similar) the intracapsular part of the periotic sac communicates freely through the laterally-placed periotic foramen with the extracapsular part of the periotic sac. The latter is situated in the space between the processus subcapsularis and the lateral wall of the otic capsule, and contributes to the formation of the secondary tympanic membrane at the fenestra pseudorotunda. It seems obvious, as de Beer suggests, that the processus subcapsularis has extended the recessus scalae tympani laterally and superiorly to the area immediately posteroventral and lateral to the plane of the fenestra ovalis. The lateral placement of the periotic foramen results in the bulk of the extracapsular part of the periotic sac being situated lateral rather than posteroinferior to the otic capsule. The ventromedial extension of the sac into relationship with the glossopharyngeal and vagus nerves, and with the meninges, leaves no doubt concerning its homology. It seems probable that this extension indicates a more posteromedial placement of the extracapsular part of the sac in more primitive forms. The extension is certainly analogous (if not homologous) to the periotic duct of the cochlear aquaeduct of mammals, and the intimacy of its relationship to both the ninth and tenth nerves seems to preclude its derivation from any form in which a definitive recessus scalae tympani was present.

Although the middle ear has been considered extensively, features of the morphology of the internal ear have never been adequately evaluated in problems of reptilian taxonomy or phylogeny. Shute and Bellairs (1953) have described the highly-developed limbic lip of geckos and pygopodids, and utilized this characteristic in suggesting affinities between these groups. In their introductory remarks they comment:

> "Although the differences observed between the inner ears of various kinds of lizards may well have some relationship to their powers of hearing, it is seldom possible to explain them in terms of adaptive modification since they have no obvious association with the habits of the forms which exhibit them. In this respect the inner ear as a whole differs from both the middle ear and the eye, which are very subject to adaptive changes, particularly in lizards where their reduction is often associated with loss of the limbs and the assumption of burrowing habits. Observations on a relatively conservative structure such as the inner ear are therefore likely to have special significance in a consideration of the phylogenetic history and affinities of the groups studied."

Although these authors refer particularly to lizards, their comments seem, in light of the evidence of this investigation, to be applicable to the inner ear of reptiles in general. A fundamental conservatism in labyrinthine organization is evident in the major taxonomic assemblages, and there is no evidence of changes which are clearly degenerative in nature. It should be noted, however, that the inability to make "obvious association" of changes in the inner ear with the known habits of the forms showing them does not preclude the possibility of such modifications being adaptive; it is probable that they cannot be appreciated as such because of our limited information concerning reptilian auditory physiology and natural history. In the absence of such information, any attempt to interpret reptilian phylogeny and affinities on the basis of auditory structure must be conservative, but there are indications that studies of the morphology of the inner ear might well augment other lines of investigation.

The major changes in the anatomy of the periotic labyrinth correspond well with generally-accepted ideas of the interrelationships of the major assemblages of reptiles. Representatives of the Chelonia, Rhynchocephalia, Squamata and Crocodilia are clearly separable on the basis of major alterations in the organization of the labyrinth, and, within the Squamata, the ophidian periotic labyrinth appears to be a direct derivative of one similar to that in modern lacertilians. Only limited inferences can be drawn concerning the origins of these ordinal groups because of lack of adequate paleontological information concerning the osteology of the otic region in primitive reptiles. As noted above, it seems probable that the periotic labyrinth of *Sphenodon* is similar to that which must have been present in captorhinomorphs, forms referred to a position near reptilian "stem stock." The Lepidosauria show relatively little intracapsular change from the presumed primitive pattern of the labyrinth, and the derivation of the extracapsular periotic relationships in the Squamata is simple and distinctive. Chelonians and crocodilians show divergent major intracapsular and extracapsular modifications of obvious antiquity; the morphology of the labyrinths of both lines can, however, be logically derived from the presumed primitive organization.

In the smaller taxonomic assemblages, several features seem worthy of note, but will require additional investigation to establish their general applicability. In those families of the Squamata represented in this study by more than one form, the periotic labyrinth (and otic labyrinth) tends to show a characteristic familial morphology. In some groups (*e. g.*, skinks and geckos) the identifying features are distinctive, while in others (*e. g.*, iguanids and lacertids) they are more subtle and involve labyrinthine relationships and proportions rather than special structures. Despite the common characteristics within families, however, differences between related genera are obvious, and there are indications that the morphology of the labyrinth is diagnostic to the level of the species. Within both the family and the genus the structures showing the greatest tendency to vary are those which are probably directly concerned with the transmission and reception of vibrations. These include the footplate, the periotic scalae and sac, the lagenar and saccular maculae, and the basilar papilla. Changes in these structures are so obvious in forms such as the skinks and geckos that they undoubtedly reflect some alteration in auditory function, but, as Shute and Bellairs (1953) observe, it is impossible to make direct correlations with the known habits of the animals showing the change.

Either positive or extensive comment on interfamilial relationships is precluded by the limited sample employed in this investigation, but some observations seem worthy of record. Intracapsular specialization in geckos is greater than indicated by Shute and Bellairs (*ibid.*) and involves both the otic and periotic labyrinths. The differences noted in labyrinthine organization in these forms tend to support Underwood's (1954) recognition of the families Eublepharidae, Sphaerodactylidae and Gekkonidae, but cast some doubt on the propriety of including *Aristelliger* in the family last named. Leptoglossan families show a series of common labyrinthine characteristics and show some evidence of progressive specialization within the infraorder. Indications of divergent progressive change in the periotic system are also found in the Iguanidae. On the whole, the morphology of the lacertilian periotic labyrinth tends to indicate at least three lines of change which correspond to the assemblages given by Romer (1956) as the Iguania, Nyctisauria and Leptoglossa. On the other hand, the known otic morphology of forms included is that author's Diploglossa cannot be interpreted at this time.

In his reports, de Burlet (1929, 1934) indicates that *Anguis* shows characteristics of the periotic system which resemble those found in *Sphenodon;* notable among these is the passage of the periotic sac through part of the cranial cavity and its projection through the vagus foramen. Such an arrangement, differing radically from that in *Ophisaurus,* might be attributed to either retention of primitive features in the inner ear, or convergence associated with loss of the tympanic cavity. *Varanus*, the only other member of the infraorder in which the anatomy of the inner ear has been investigated in some detail, shows resemblances to *Ophisaurus,* but is unusual in that an accessory scala tympani is developed. These findings certainly seem to substantiate Romer's (1956) observation that, ". . . the group (Diploglossa) is a very diverse one, and its naturalness might be questioned." Furthermore, it seems probable that an intensive study of otic morphology might contribute significantly to clarification of the affinities which exist within the group.

In the absence of experimental studies dealing directly with the manner in which the periotic labyrinth functions in reptiles, two concepts are to be found either stated or implied in the literature dealing with the reptilian ear. One, quite positively stated by de Burlet (1934), holds that vibrations introduced into the periotic cistern by the footplate traverse the full length of the periotic channels, stimulate the basilar papilla as they pass in relationship to the basilar membrane, and are finally dampened at the peripheral extremity of the periotic sac. Conversely, Wever and Vernon (1956) unquestioningly assume that vibrations traverse the periotic cistern, cochlear duct and periotic sac in sequence, stimulating the basilar papilla in their passage through the duct. The same concept is implied by Shute and Bellairs (1953) when they state, ". . . the anterior half of the papilla basilaris lies in the direct line of fluid impulses transmitted across the perilymphatic cistern and cochlear duct from the footplate of the stapes." The second view conforms to current thinking concerning the mode of transmission of vibrations through the mammalian cochlea, and finds considerable support in Tonndorf's (1959) report of experiments in which models (resembling the reptilian inner ear) were used to study the transfer of energy across the cochlea.

The morphological information accumulated here lends indirect support to the concept of direct transmission of energy through the inner ear in reptiles. In all forms other than crocodilians, the major part of the basilar papilla would be encompassed by lines projected from the margins of the footplate to the margins of the periotic foramen. In those forms in which the periotic foramen lies directly opposite the footplate, the peripheral attachments of the latter are of a nature that suggests a pistonlike movement in normal function; in those in which the foramen is not aligned with the footplate but (usually) posterior to it, one part (usually anterior) of the fibrous peripheral attachment is lax and suggests that the movement of the footplate would be of a "rocking" or "hinged" type. Both of these arrangements would result in the propagation of cisternal pressure waves in which the maximal displacement (and energy) would be directed toward the basilar papilla and periotic foramen. In no form does the vestibular membrane seem to be sufficiently thick to impede direct transmission of vibratory movement from the fluid of the periotic cistern to the otic fluid of the cochlear duct. On the strength of these relationships alone, a strong case can be made for vibrations introduced at the footplate traversing the periotic cistern, vestibular membrane and otic fluid of the cochlear duct, then distorting the tectorial membrane, basilar papilla and basilar membrane as they are transmitted toward the periotic sac and final dampening. Such reasoning does not, however, completely negate the possibility of transmission of vibrations along the circuitous route formed by the periotic channels. Such a concept does seem to be obviated by the relationships found in forms in which an accessory scala tympani is present. In these, vibrations carried along the full length of the periotic channels would conceivably reach those parts of the basilar membrane contacted by the accessory scala (assuming that decay in their original energy content had not rendered them valueless as a stimulus), but would find themselves "trapped" in the sense that no release or dampening route exists at the distal extremity of the accessory scala tympani; thus, all residual energy would necessarily be transferred through the basilar membrane into the otic fluid, a situation which seems entirely incompatible with efficient functioning of the fluid system. On the other hand, the accessory scala forms a logical and efficient pathway for the conduction of vibrations from the cochlear duct to the dampening structures at the periphery of the periotic sac. These concepts are diagrammatically represented in Figures 53 and 54. It should be noted that, in those forms showing much elongation of the basilar papilla, pressure waves transmitted directly from the footplate to the periotic foramen would efficiently stimulate only that part of the papilla opposite the foramen; such relationships suggest that energy transfer may involve the formation of both pressure waves and traveling waves, and occur in a fashion similar to that elucidated by Tonndorf (1959). Invocation of such an explanation is particularly necessary in crocodilians.

The function of the reptilian basilar papilla as an auditory receptor is firmly established, but questions exist concerning the functions of the lagenar and saccular maculae. There is some agreement that the latter probably has a role in audition (de Burlet 1929, 1934; Weston, 1939), but expressed opinions concerning the function of the lagenar macula are rare. Weston (*ibid.*) attributes an auditory function to the receptor and suggests that it (together with the saccular macula) may operate in reception differing qualitatively from that of the basilar papilla. No suggestion is offered concerning a possible route for vibratory stimuli to reach the maculae, but tacit agreement with de Burlet (1934) is implied. The latter rules out the possibility of conduction of vibrations to the lagenar macula by the periotic fluid, and considers only the basilar papilla to be a periotic receptor (perilymphatische Sinnesendstelle) in reptiles.

In the forms utilized in this investigation, the lagenar part of the cochlear duct is, invariably, directly related to some part of the lateral body of periotic fluid (periotic cistern and/or its extensions); a similar situation exists in the case of the saccule. The common relationship is one in which the periotic contact is made opposite the macula and its overlying otolith, usually at the thin lateral walls of the saccule and cochlear duct. This relationship is in itself suggestive of a functional association between impulses propagated in the periotic fluid and the maculae. Additional support for such an interpretation is found in the extensions of the lateral fluid body developed in those forms in which direct relationship with the periotic cistern or scala vestibuli does not exist. The scala lagenae is a relatively constant feature, but is developed only to the extent required for full periotic relationship to the lagena. The scala sacculi, more striking in its departure from the usual periotic pattern, is best developed as a discrete channel in those forms in which the normal lateral association of the saccule with the periotic cistern is lost. The variable morphology noted suggests that the channel may function differently in different forms; in practically all cases, however, it can be interpreted functionally only as a fluid pathway for the transmission of vibratory stimuli. I submit, therefore, that the saccular and lagenar maculae in reptiles not only subserve a function in the reception of vibratory stimuli, but that they are also periotic receptors. There is no question that their auditory function differs from that of the basilar papilla, since the otolithic mass associated with each would hardly be adapted to analysis of complex sounds; furthermore, this is not intended to suggest that audition is the sole macular function. Subjectively, it appears that the basilar papilla, the saccular macula and the lagenar macula constitute an auditory triad; the basilar papilla probably functions in analytical reception of sounds, and the maculae in non-analytical reception. The tendency of the three receptor areas to vary in size interdependently, as noted above and reported by Weston (1939), lends support to this interpretation. It would, indeed, be interesting to know if associations of the relative sizes of these receptors could be made with the habits and habitats of a variety of forms.

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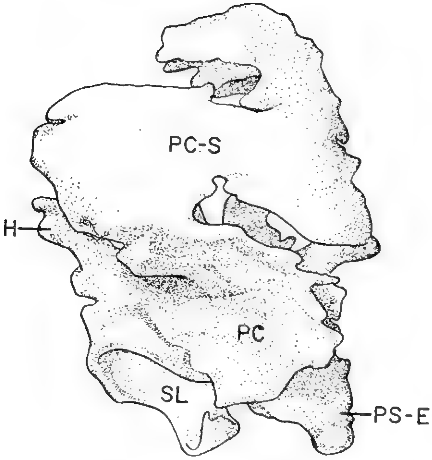
KEY TO ABBREVIATIONS

AOA—anterior otic ampulla
ASD—anterior semicircular duct
AST—accessory scala tympani
BP—basilar papilla
CD—cochlear duct
CS—cisternal septum
DR—ductus reuniens
FP—footplate of columella auris
H—helicotrema
JS—juxtastapedial sinus
L—lagena
Lb—limbus
LOA—lateral otic ampulla
LSD—lateral semicircular duct
MC—meningeal contact of periotic sac at medial aperture of the recessus scalae tympani
ML—macula lagenae
MS—macula sacculi
OC—otic capsule
OD—otic duct
PC—periotic cistern
PC-S—saccular part of periotic cistern
PCS—paracapsular sinus
PF—periotic foramen
POA—posterior otic ampulla
PS—periotic sac
PS-I—intracapsular part of periotic sac
PS-E—extracapsular part of periotic sac
PSD—posterior semicircular duct
S—saccule
SCP—subcapsular process
SL—scala lagenae
SS—scala sacculi
ST—scala tympani
STM—secondary tympanic membrane
SV—scala vestibuli
U—utricle
USD—utriculo-saccular duct
VIII—acoustic nerve
IX—glossopharyngeal nerve
X—vagus nerve



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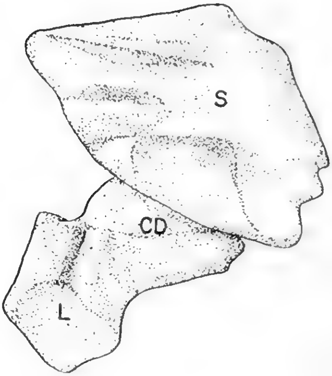

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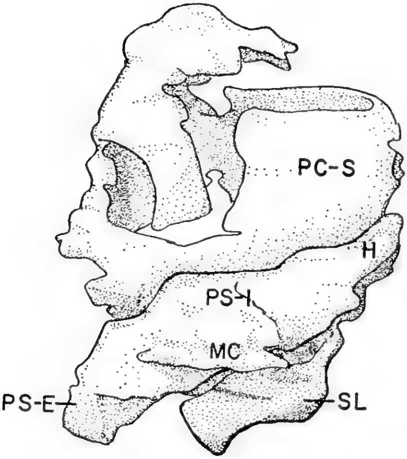

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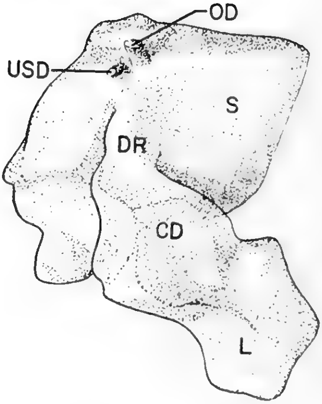


6.

Reconstructions of the Inferior Divisions of the Labyrinths of *Sphenodon*

FIG. 3. Lateral view of the left periotic labyrinth of a late embryo. 29×

FIG. 4. Lateral view of the left saccule and cochlear duct of a late embryo. 29×

FIG. 5. Medial view of the left periotic labyrinth of a late embryo. 29×

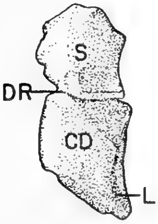
FIG. 6. Medial view of the left saccule and cochlear duct of a late embryo. 29×

FIGURES 7-14

Reconstructions of the Inferior Divisions of the Labyrinths of Iguanid Lizards

FIG. 7. Lateral view of the right saccule and cochlear duct of *Anolis*. 17×
FIG. 8. Lateral view of the right periotic labyrinth of *Anolis*. 17×
FIG. 9. Medial view of the right saccule and cochlear duct of *Anolis*. 17×
FIG. 10. Medial view of the right periotic labyrinth of *Anolis*. 17×
FIG. 11. Lateral view of the left periotic labyrinth of *Phrynosoma*. 17×
FIG. 12. Medial view of the left periotic labyrinth of *Phrynosoma*. 17×
FIG. 13. Lateral view of the left periotic labyrinth of *Crotaphytus*. 17×
FIG. 14. Medial view of the left periotic labyrinth of *Crotaphytus*. 17×

Figures 7-14



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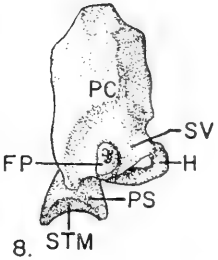

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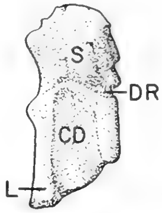

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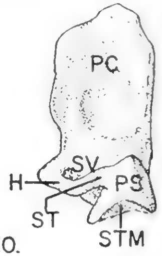

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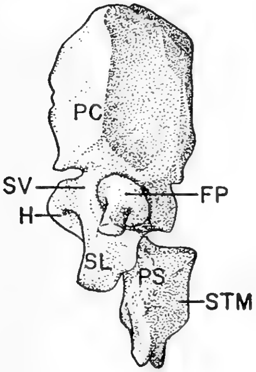

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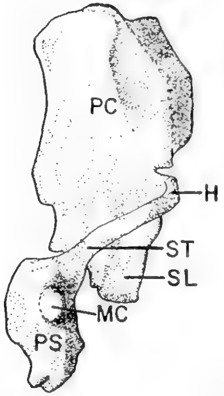

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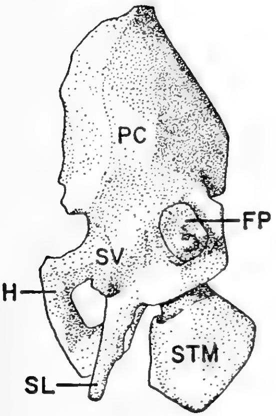

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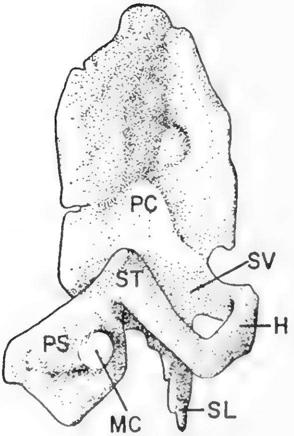

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FIGURES 15-20

Reconstructions of the Inferior Divisions of the Labyrinths of Gekkonoid Lizards

FIG. 15. Lateral view of the left periotic labyrinth of *Coleonyx*. 22×

FIG. 16. Medial view of the left periotic labyrinth of *Coleonyx*. 22×

FIG. 17. Medial view of the left saccule and cochlear duct of a late embryo of *Aristelliger*. 25×

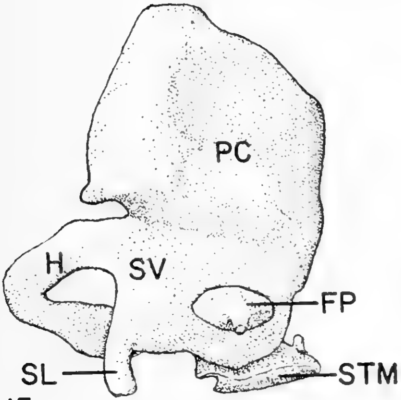
FIG. 18. Medial view of the left periotic labyrinth of a late embryo of *Aristelliger*. 25×

Note opening in periotic cistern resulting from laterally expanded saccule, and the incomplete development of the scala sacculi.

FIG. 19. Lateral view of the left periotic labyrinth of *Hemidactylus*. 22×

FIG. 20. Medial view of the left periotic labyrinth of *Hemidactylus*. 22×

FIGURES 15-20



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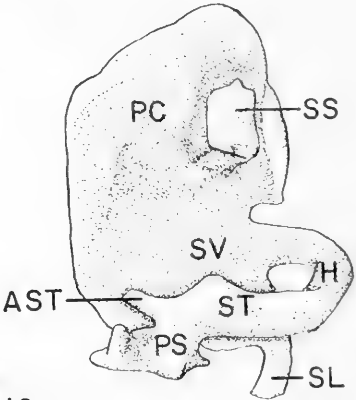

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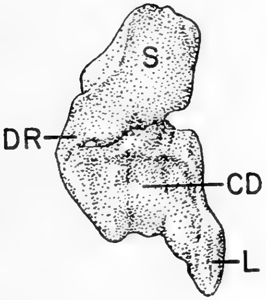

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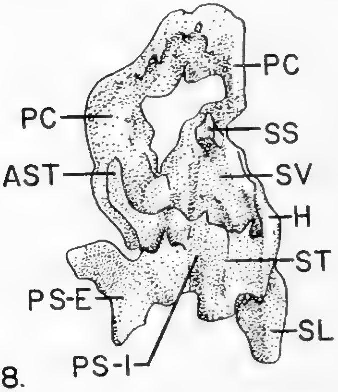

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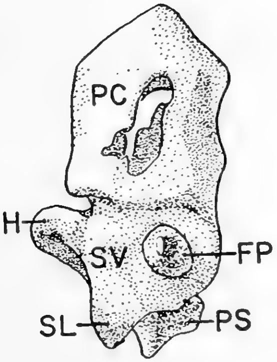

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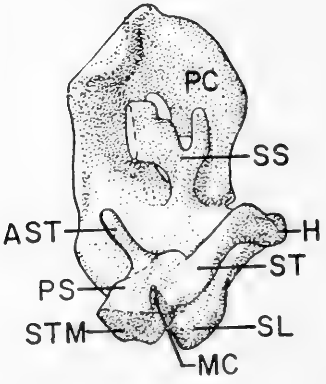

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FIGURES 21-31

Reconstructions of the Inferior Divisions of the Labyrinths of Leptoglossans

FIG. 21. Lateral view of the left periotic labyrinth of *Cnemidophorus.* 14×

FIG. 22. Medial view of the left saccule and cochlear duct of *Cnemidophorus.* 14×

FIG. 23. Medial view of the left periotic labyrinth of *Cnemidophorus.* 14×

FIG. 24. Lateral view of the left periotic labyrinth of *Eumeces obsoletus.* 14×

FIG. 25. Medial view of the left saccule and cochlear duct of *E. obsoletus.* 14×

FIG. 26. Medial view of the left periotic labyrinth of *E. obsoletus.* 14×

FIG. 27. Lateral view of the left periotic labyrinth of *Eumeces fasciatus.* 14×

FIG. 28. Medial view of the left periotic labyrinth of *E. fasciatus.* 14×
Note obvious differences of parts from those in *E. obsoletus.*

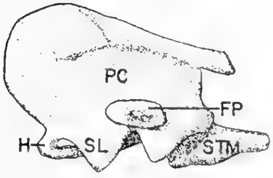
FIG. 29. Lateral view of the left periotic labyrinth of a late embryo of *Lacerta.* 22×

FIG. 30. Medial view of the left saccule and cochlear duct of a late embryo of *Lacerta.* 22×

FIG. 31. Medial view of the left periotic labyrinth of a late embryo of *Lacerta.* 22×

Note development of saccular part of the periotic cistern and absence of a scala sacculi at this stage.

FIGURES 21-31



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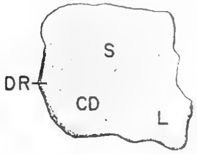

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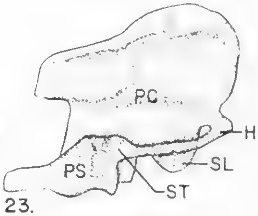

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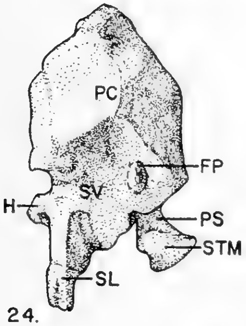

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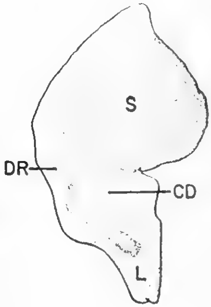

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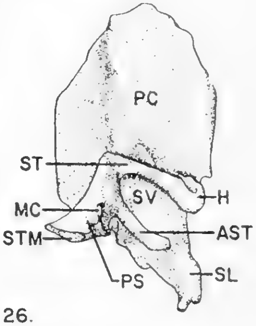

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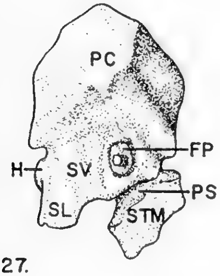

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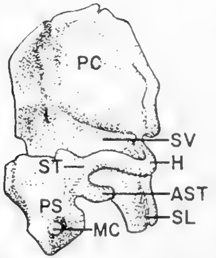

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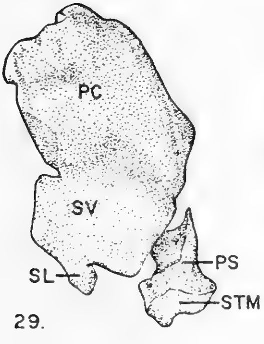

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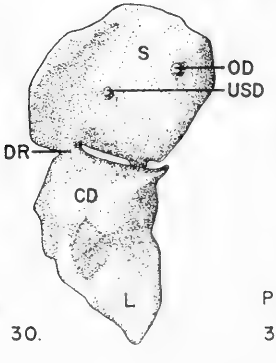

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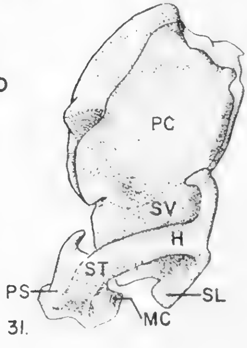


31.

FIGURES 32-37

Reconstructions of the Inferior Divisions of the Labyrinths of Diploglossans

FIG. 32. Lateral view of the left periotic labyrinth of *Ophisaurus*. 13×

FIG. 33. Medial view of the left saccule and cochlear duct of *Ophisaurus*. 13×

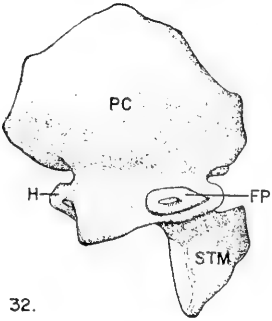
FIG. 34. Medial view of the left periotic labyrinth of *Ophisaurus*. 13×

FIG. 35. Medial view of the left saccule and cochlear duct of *Varanus*. 13×

FIG. 36. Lateral view of the left periotic labyrinth of *Varanus*. 13×

FIG. 37. Medial view of the left periotic labyrinth of *Varanus*. 13×

FIGURES 32-37



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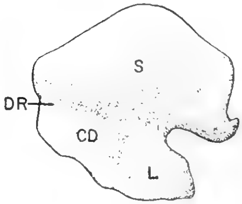

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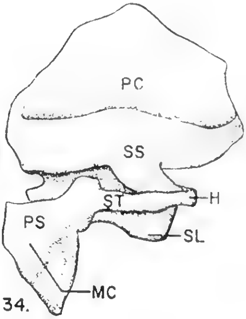

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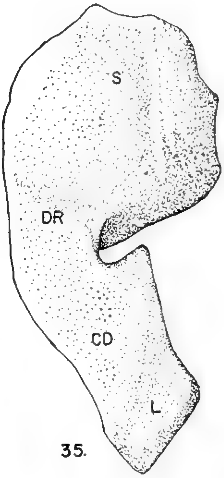

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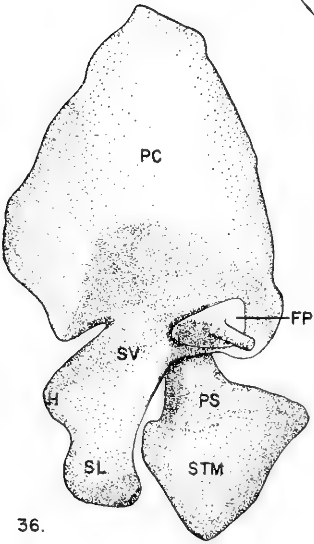

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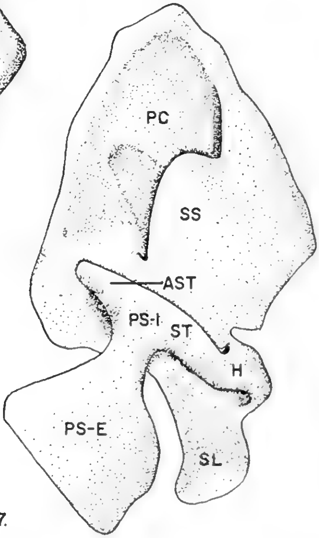


37.

Figures 38-41

Some Auditory Structures of Colubrid Snakes

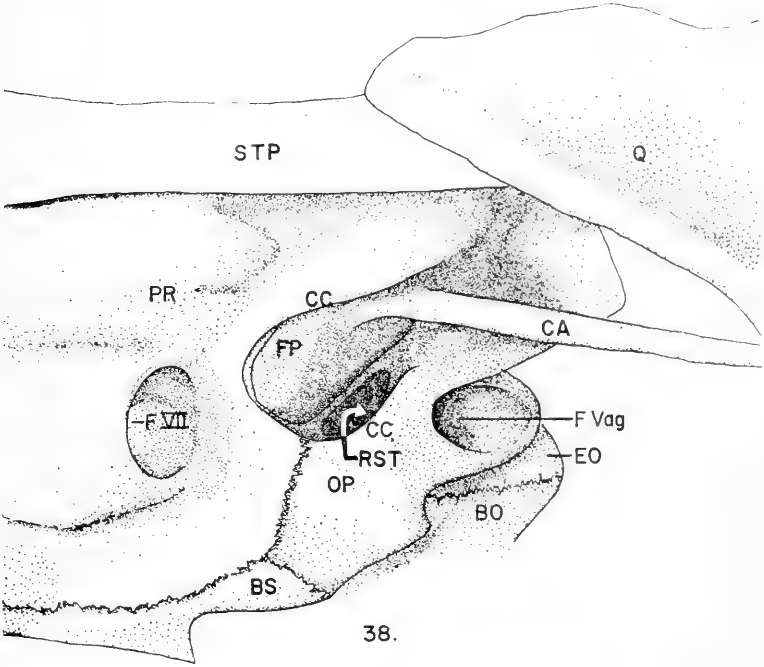
Fig. 38. Lateral view of the left otic region in a skull of *Thamnophis*. 23 × BO-basioccipital; BS-basisphenoid; CA-columella auris; CC-circumfenestral crest; EO-exoccipital; FVag-vagus foramen; FVII-foramen of facial nerve (part); OP-opisthotic; PR-prootic; Q-quadrate; RST-recessus scalae tympani; STP-supratemporal; FP-footplate. Note the juxtastapedial fossa (unlabeled) delimited by the circumfenestral crest.

Fig. 39. Medial view of a reconstruction of the left saccule and cochlear duct of *Diadophis*. 33×

Fig. 40. Lateral view of a reconstruction of the inferior division of the left periotic labyrinth of *Diadophis*. 33×

Fig. 41. Medial view of a reconstruction of the inferior division of the left periotic labyrinth of *Diadophis*. 33×

FIGURES 38-41



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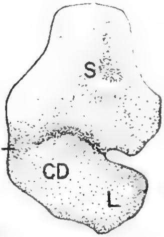

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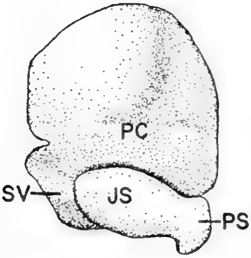

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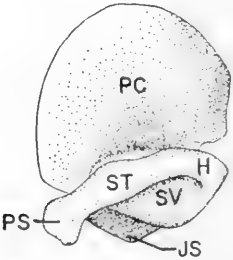

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FIGURES 42-45

Reconstructions of the Inferior Divisions of the Labyrinths and Paracapsular Sinus of *Chrysemys*

Fig. 42. Lateral view of the left saccule and cochlear duct of a late embryo. 40×

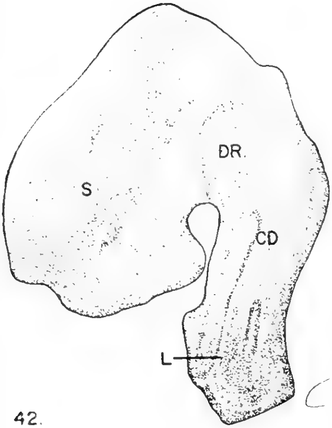
Fig. 43. Lateral view of the inferior division of the left periotic labyrinth of a late embryo. 40×

Outline of paracapsular sinus shows its relationship to periotic structures, and the base of the canal (arrow) which connects right and left sinuses in the embryo.

Fig. 44. Medial view of the left saccule and cochlear duct of a late embryo. 40×

Fig. 45. Medial view of the inferior division of the left periotic labyrinth and paracapsular sinus of a late embryo. 40×

FIGURES 42-45



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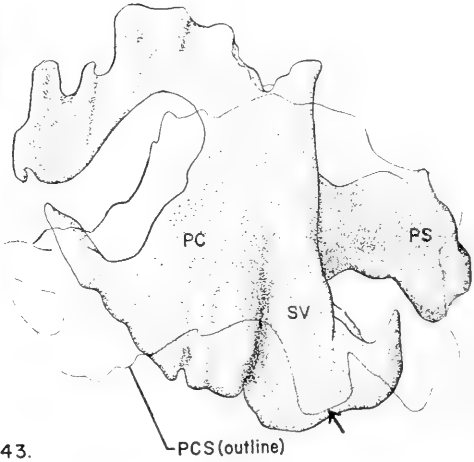

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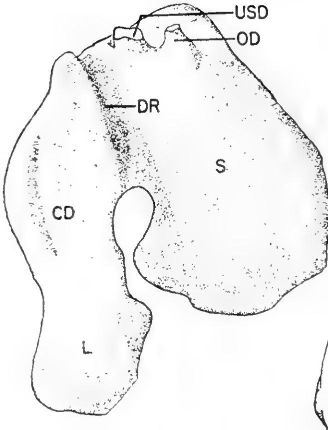

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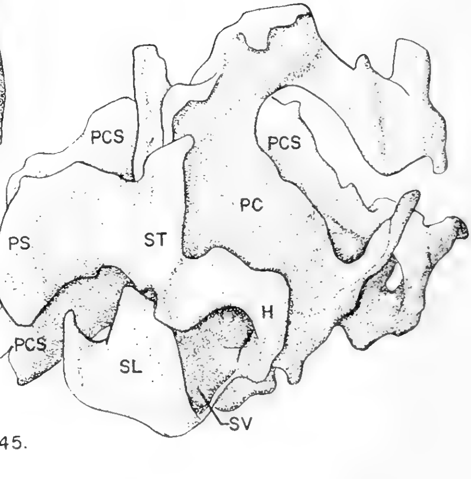

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FIGURES 46-54

Schematic Representations of the Internal Ear in Several Reptiles

FIG. 46. Lateral view into the inner ear of a crocodylid; footplate and periotic foramen are superimposed to show relationships.

Note small accessory scala tympani (unlabeled) invading limbus at each extremity of the basilar membrane.

FIG. 47. Transverse section through the footplate and periotic foramen in a crocodylid.

Note free extension of periotic sac through periotic foramen into the recessus scalae tympani.

FIG. 48. Frontal section through the inner ear of *Sphenodon*.

FIG. 49. Frontal section through the inner ear of a chelonian.

FIG. 50. Frontal section through the inner ear of a colubrid snake.

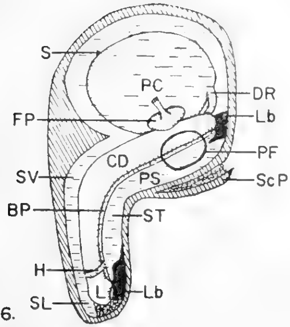
FIG. 51. Transverse section through the inner ear of a lacertilian in which the secondary tympanic membrane is situated deep in the recessus scalae tympani.

FIG. 52. Transverse section through the inner ear of a lacertilian in which the periotic sac fills the recessus scalae tympani.

FIG. 53. Frontal section through the inner ear of a scincid illustrating transmission of energy according to the concept cited by de Burlet (1934). Note "trapping" of energy in accessory scala tympani.

FIG. 54. Frontal section through the inner ear of a scincid illustrating the concept of direct transmission of energy.

FIGURES 46-54



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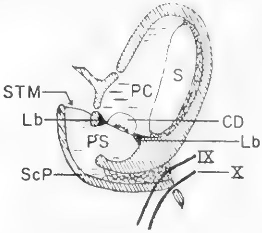

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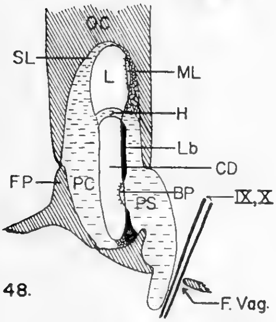

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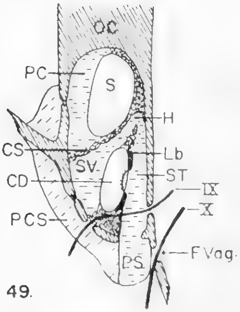

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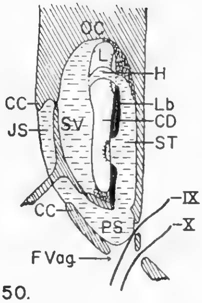

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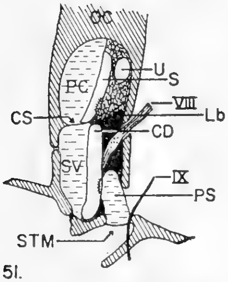

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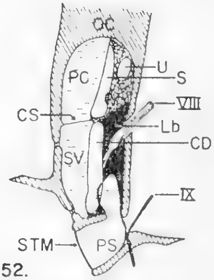

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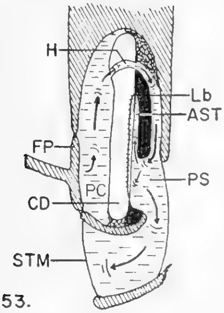

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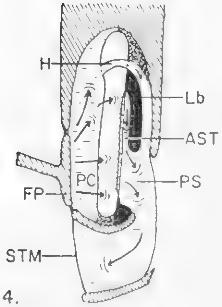

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SCIENCE BULLETIN

Vol. XLI] December 23, 1960 [No. 10

Observations on the Morphology of the Inner Ear in Certain Gekkonoid Lizards

BY

David Whitman Hamilton

Abstract: The morphology of the inner ear in ten species of gekkonoid lizards, representative of three families, is described and discussed. A ridge from the lateral wall of the otic capsule that projects into the capsule is found to be common among the gekkonoids studied; the term inferior cisternal crest is applied to it. A similar superior projection is termed the superior cisternal crest. The periotic system presents clearly-defined channels in relation to the footplate of the columella auris and the auditory receptors. Definite periotic channels are observed in relation to the sensory areas of the saccule and lagena. The periotic connective tissue in the vicinity of the medial wall of the cochlear duct is shown to be modified in the gekkonoids to form a limbus with a large dorsal projection, the limbic lip. A fault in the body of the limbus in the vicinity of the basilar papilla is termed, here, the limbic hiatus. The otic system in gekkonoid lizards exhibits differences that can be correlated with the taxonomy and phylogeny of the group to some extent; the Sphaerodactylidae are easily delineated taxonomically from the other gekkonoids on the basis of inner ear structure. The sensory areas of the saccule and cochlear duct exhibit trends that can be correlated with phylogenetic patterns noted for other aspects of the inner ear. It is probable that the inner ear in gekkonoid lizards was derived from that of a primitive stock and developed independently along three familial lines. The inner ear in pygopodoids, possibly, also arose from this same stock.

INTRODUCTION

The morphology of the inner ear of reptiles has been the subject of considerable investigation during the past century. Notable contributions have been made by Retzius (1884), Wiedersheim (1875), de Burlet (1929, 1934), and Shute and Bellairs (1953) have compared certain features of the internal ear in gekkonoids and pygopodoids and noted affinities in the inner ears of these groups. To date, however, no intensive comparative studies of the inner ear have been made in well-defined small assemblages of reptiles, and little attention has been paid to its modifications and phylogenetic significance in such assemblages.

My own preliminary study has shown that there are, within the Reptilia certain aspects of the morphology of the saccule and saccular derivatives that might elucidate interrelationships within the class. The gekkonoids appear to constitute a relatively clearly defined assemblage which shows considerable diversity in the structure of the ear; they, therefore, were chosen as a group in which the significance of the area might be evaluated.

The purpose of this study is (1) to describe the morphology of the auditory portions of the inner ear in certain gekkonoid lizards; (2) to interrelate the findings among the genera studied in order to (3) speculate on the significance of the area with respect to phylogeny within the group; and (4) to correlate these speculations with other work that has been done on different morphological areas.

I wish to express my gratitude for the assistance given by Dr. Irwin L. Baird in the preparation of this paper. Without his encouragement and criticism the project would not have been started and this paper would not have been completed.

Certain valuable specimens were supplied by Mr. Garth Underwood of the University College of the West Indies, Dr. Ernest E. Williams of the Museum of Comparative Zoology at Harvard University and Dr. John Legler, formerly of the Museum of Natural History at the University of Kansas; I wish to thank all of these gentlemen. Recognition is due, also, to Miss Diane Allen for work done in preparation of some of the figures.

MATERIALS AND METHODS

Young or adult representatives of nine genera of gekkonoids, comprising representatives from each of the three families suggested by Underwood (1954), were available for this study. Those specimens obtained from the Museum of Natural History at the University of Kansas are designated KUMNH, and those from the Museum of Comparative Zoology are designated MCZ; forms not designated were obtained either from Mr. Underwood, or by purchase from biological supply houses. The forms used are listed below:

Eublepharidae
  Coleonyx variegatus
  Coleonyx brevis
Sphaerodactylidae
  Gonatodes fuscus (KUMNH 34571)
  Sphaerodactylus macrolepsis
  Lepidoblepharis xanthostigma (MCZ 55099)

Gekkonidae
  Hemidactylus mabouia
  Phyllodactylus homolepidurus (KUMNH, unnumbered)
  Thecadactylus rapicauda (MCZ 6066)
  Aristelliger praesignis (MCZ, unnumbered)
  Gymnodactylus kotschyi (MCZ 38448)

The heads were removed, decalcified electrolytically, embedded in Hercules low viscosity nitrocellulose, and serially sectioned. The sections were mounted on slides and stained with a modification of the Mallory (1938) aniline-blue collagen stain. Using selected slides, wax reconstructions were made of portions of the otic labyrinth in some genera.

TERMINOLOGY

In recent years there has been some trend toward uniformity in the terminology applied to the inner ear. Streeter (1918) proposed that the less-cumbersome terms otic and periotic be substituted for endolymphatic and perilymphatic, respectively. This has received some recognition, and the terms are employed by Bast and Anson (1949) and others working primarily with mammals. There is, however, considerable confusion in the terminology applied to the ear in forms other than mammals; for this reason, it seems necessary to stipulate the terminology to be used in this paper.

In reptiles, as in mammals, the membranous portion of the inner ear is contained within a bony (or partially cartilaginous) receptacle termed the *otic capsule*. The cavity within the capsule is divided into superior and inferior parts, termed *vestibule* and *cochlear recess*, respectively. The vestibule contains the *saccule*, the *utricle* and the utricular extremities of the *otic semicircular ducts.*

The saccule occupies a considerable part of the vestibule. From the anteromedial wall of the saccule, the *otic duct* (endolymphatic duct) courses inferomedially beneath the utricle to exit from the otic capsule and end intracranially and intradurally in the blind *otic sac* (endolymphatic sac). A shorter duct, the *sacculo-utricular duct,* connects the saccule and utricle and usually is found at about the same horizontal level as the otic duct. Inferior to these ducts a specialized area of neuroepithelium, the *saccular macula,* occupies a part of the medial saccular wall, and has associated with it the large saccular otolith that occupies a considerable part of the saccular cavity.

A membrane, the *cisternal septum* (Baird, 1960), continuous with the membrana propria of the saccule and the internal periosteum of the otic capsule, stretches from the inferior margin of the saccule to the lateral bony wall of the otic capsule. The posterior limit of this membrane is, in gekkonoids, superior to the footplate of the columella auris.

From the region of the posteroinferior saccular margin, the *sacculo-cochlear duct* (ductus reuniens) is given off and becomes continuous with the *cochlear duct* housed in the cochlear recess.

The cochlear duct is a roughly pyramidal diverticulum of the saccule. The anteroinferior region of the cochlear duct is termed the *lagena* and is contained in its own part of the cochlear recess, the *lagenar recess.* The cochlear duct, taken as a whole, contains two neuroepithelial sensory areas. The *lagenar macula* occupies parts of the walls of the lagena; this receptor is variable in size and shape, and may occupy a considerable area of either the medial or lateral lagenar wall, or both. There has been some question concerning the function of this particular receptor (de Burlet, 1929, 1934; Weston, 1939). These authors (and others) suggest that some auditory function may be attributed to the macula, but offer no comments concerning how this is achieved. Recently, Baird (1960) has pointed out that an extension of the periotic system invariably associates itself with this macula in reptiles, as Weston (1939) has noted in *Echidna*, and suggests that it is a periotic receptor (perilymphatische Sinnesendstelle of de Burlet, 1934).

The *basilar papilla* is the so-called functional, or auditory, part of the cochlear sensory area and is homologous, at least in part, to the mammalian organ of Corti. It rests upon the *basilar membrane,* which is supported by a ring of rather dense connective tissue called the *limbus.* The latter is situated medially in the cochlear recess adjacent (in part) to the medial wall of the cochlear duct. The term, limbus (suggested for use in reptiles by Shute and Bellairs, 1953), is taken from mammalian nomenclature, and actually designates the presumed homolog of the mammalian limbus and triangular ligament. In gekkonoids, pygopodoids and at least one teiid, the limbus has a falciform extension, the *limbic lip* (Shute and Bellairs, *ibid.*), which projects into the cavity of the cochlear duct. This structure was described by de Burlet (1934) and labelled "labium vestibuli" in a figure representing a transverse section through the inner ear of *Gecko.* He says of that structure:

> "Oberhalb der Membrana basilaris und der Papilla basilaris buchtet sich ein hakenförmig gekrümmter Fortsatz in das Innere des Ductus cochlearis hinein (Abb. 1177), dessen Ende trägt die Membrana tectoria, welche stets vorhanden ist."

Attached to this is the *tectorial membrane*, a cuticular lamina which extends toward, and appears to rest upon, the hair cells of the basilar papilla.

The lateral wall of the cochlear duct is termed the *vestibular membrane* (tegmentum vasculosum); this is generally thin in comparison to the basilar membrane, but in certain gekkonoids it tends to be rather thick.

The terms applied by Baird (1960) to the periotic system in reptiles seem quite reasonable and are applicable, in general, in all reptiles. He states that the periotic labyrinth is histologically comprised of three parts:

(1) a *membrana propria* investing the epithelial otic labyrinth,
(2) the *internal periosteum* of the otic capsule, and
(3) the *periotic reticulum*.

The *periotic fluid* is contained between the membrana propria and the internal periosteum, and is associated with all of the otic labyrinth including the utricle and the otic semicircular ducts and ampullae. For the part of the periotic labyrinth surrounding the latter structures, the terms periotic semicircular canals and periotic ampullae are used.

The part of the periotic system surrounding and adjacent to the saccule and cochlear duct can be divided into different morphological areas to which the following terms have been applied:

(1) That part "internal to the columella auris . . . (and lateral to) . . . the wall of the proximal end of the cochlear duct, the ductus reuniens (sacculo-cochlear duct) and the lateral wall of the saccule, . . ." comprising a common cavity, is termed the *periotic cistern*.

(2) An anteriorly-directed extension of the cistern is termed the *scala vestibuli*.

(3) An antero-inferior projection of the scala vestibuli is termed the *scala lagenae*.

(4) An inconstant diverticulum, which arises from the scala vestibuli, extends superiorly between the cochlear duct and the saccule and comes into direct relation to the macula sacculi, is termed the *scala sacculi*.

(5) The periotic channel curving around the anterior margin of the cochlear duct is termed the *helicotrema* (part of the perilymphatic duct of other workers).

(6) The helicotrema can extend medially into a duct, the *scala tympani*, or empty directly, on the medial side of the cochlea, into the *periotic sac*, which is associated with the basilar membrane.

(7) From the posterosuperior surface of the latter, a diverticulum extends posteriorly in intimate relationship to the posterior part of the basilar membrane. This is termed the *accessory scala tympani*, and is found in most gekkonoid lizards.

THE AUDITORY PART OF THE INNER EAR IN GEKKONOID LIZARDS

Eublepharidae

(Figs. 1-3)

According to Underwood (1954), the Eublepharidae range around the world between the equator and the northern temperate zone. The family is small, with but five genera, and only *Coleonyx* is found in the United States; representatives of two species of that genus were available for study.

The partially bony, partially cartilaginous otic capsule of *Coleonyx* contains two major cavities; superiorly is a large vestibule and inferiorly is the cochlear recess. This division is arbitrary for the two cavities communicate freely.

Laterally, the vestibule is limited by a smooth, concave bony wall. Inferiorly, the lateral wall of the vestibule terminates in a horizontal, medially-projecting ridge of bone superior to the footplate of the columella. Most apparent anterolaterally, this ridge forms part of the superior wall of the scala vestibuli and blends anteriorly into the bony canal which houses the helicotrema. Posteriorly, the ridge is less prominent and can be identified only to the level of the shaft of the columella auris. I can find no name applied to this structure in the literature; it is proposed, therefore, that this ridge be called the *inferior cisternal crest*.

Superiorly, the lateral wall of the vestibule ends in a second longitudinal ridge. This ridge becomes apparent anteriorly just posterior and superior to the location of the ampulla of the anterior semicircular duct. It extends posteriorly to terminate in the lateral bony wall of the medial limb of the horizontal semicircular canal. Approximately in the middle of the vestibule the ridge forms the lateral lamina of the *foramen of the superior sinus* (foramen pro sinu superiore of de Beer, 1937). It is proposed that this ridge be called the *superior cisternal crest.*

The medial wall of the vestibule is concave anteriorly, but essentially flat and inclined medially throughout the greater part of its extent. It forms part of the lateral wall of the cranial cavity and is perforated by the aquaeduct of the vestibule, which is situated at the junction of the flattened and concave parts of the wall. The inferior limit of the medial wall may be said, arbitrarily, to lie at the level of the superior margin of the internal acoustic foramen. Thus, a plane passing medially from the inferior cisternal crest to the level mentioned above would establish the division of the vestibule from the cochlear recess.

The cochlear recess has the form of an elongate inverted pyramid; the lagenar recess forms a small anteroinferior outpocketing of the cochlear recess. Midway along the horizontal axis of the lateral wall is the *oval window* (fenestra ovalis). In this genus, the opening is greatly elongated longitudinally and occupies two-thirds of the anteroposterior length of the cochlear recess. Into the oval window is fitted the footplate of the columella auris. The footplate is attached eccentrically to the shaft; considerably more of its area is located anterior to the columellar shaft than posterior to it. The shaft slopes posteroinferiorly to its attachment to the tympanic membrane. The shape and positioning of the columella relative to inner ear structures possibly has some bearing on the transmission of vibrations. Determination of the extent of this influence is beyond the scope of this paper, but investigation of the question has begun.

Two openings are present in the medial wall of the cochlear recess. Anteriorly is the *internal acoustic foramen*, and, opposite the anterior limit of the oval window, the periotic foramen connects the cochlear recess with the *recessus scalae tympani.* There are two apertures from the latter. The *medial aperture,* facing the cranial vault, is divided by a vertical strut of bone; the entire opening is closed by meninges and periotic membranes, but the ninth cranial nerve does perforate these membranes and exit from the more posterior opening. The *lateral aperture* faces the tympanic cavity inferior to the oval window.

The saccule of *Coleonyx,* small and centrally placed in the vestibule, is roughly trapezoidal when viewed from the lateral aspect. Its inferior margin is directed slightly lateral and, anteriorly, slightly overlaps the superior margin of the cochlear duct. This results in obliquity of placement within the vestibule in two planes, since the entire anterior part of the structure is displaced laterally.

The medial wall of the saccule is composed of epithelium supported upon a condensation of periotic connective tissue. In *C. variegatus* this condensation is well organized although not particularly thick; in *C. brevis* it is denser, thicker and presents a more solid appearance. The generalized epithelium of the medial wall is low, cuboidal and restricted to the periphery; centrally the greater part of the wall is occupied by the saccular macula. This sensory area appears posteriorly as a rather narrow strip of neuroepithelial cells in the middle third of the medial wall, and continues anteriorly for approximately three-fourths of the length of the saccule. Anteriorly the strip expands vertically to include most of the medial wall, except for the most superior and inferior parts. The macula is shaped like a teardrop and comprises about 17 percent of the total sacculo-cochlear sensory area.

Dorsal to the saccular macula, at the junction of the anterior and middle thirds of the saccule, the otic duct empties into the saccular cavity by way of an expanded sinusoidal portion. This is a continuation of the main duct, which courses beneath the utricle, traverses the vestibular aquaeduct and ends in the expanded otic sac. Just posterior to the entry of the otic duct, at the same horizontal level, the sacculo-utricular duct joins the saccule and utricle.

The lateral saccular wall is decidedly thinner than the medial. Its epithelium is squamous and the membrana propria, for the most part, is thin and wispy in both species of *Coleonyx* examined. Abutting against the lateral saccular wall, apparently within the saccular cavity and located directly opposite the hair cells of the saccular macula, is a dense, highly-organized conglomerate of connective tissue that appears to be an elaboration of the membrana propria of the wall. In *C. brevis* the mass is large; in *C. variegatus* it is decidedly smaller. The lateral saccular wall does not come into close relationship with the wall of the vestibule; they are separated by a distinct periotic space.

Posteriorly, the saccule tapers into the sacculo-cochlear duct which is large, cylindrical and vertical. The duct joins the saccule to the roughly rectangular cochlear duct. The latter is large, approximately as long as it is tall and is located medially in the cochlear recess. Its lateral wall, the vestibular membrane, is composed of the epithelium of the cochlear duct supported upon periotic connective tissue, within which there are a number of blood vessels. The vestibular membrane, although distinct, is thin and of approximately the same thickness as the lateral saccular wall. The periotic connective tissue of the inferior and superior cochlear margins resembles that associated with the medial wall of the saccule; in places the connective tissue of the superior wall blends into that of the saccular wall. The greater part of the medial cochlear wall is intimately associated with (or incorporates) a specialization of the periotic connective tissue called the limbus.

The limbus is a rather thick, ovoid plate of tissue which abuts against the medial wall of the cochlear recess and is pierced by an opening occupied by the basilar membrane. This opening, generally oval, is labelled "aperture in limbus for basilar membrane" in the figures of Shute and Bellairs (1953). For the sake of convenience a less unwieldy term seems desirable; it is proposed, therefore, that the term *limbic hiatus* be applied to this aperture.

The limbic tissue surrounding the limbic hiatus is of great density; peripheral to this the organization is looser and grades in resemblence toward that adjacent to the medial saccular wall. The limbus begins posteriorly at the cochlear end of the sacculo-cochlear duct and extends anteroinferiorly almost to the end of the cochlear duct. Arising laterally from the limbus and extending into the cochlear cavity is the limbic lip. This arises posteriorly from the dorsal part of the limbus as a rather small and delicate extension and continues anteroinferiorly to become massive and form a "U-shaped" sulcus (*cochlear sulcus* of Shute and Bellairs, 1953) with the main body of the plate. The cochlear sulcus is deeper anteriorly than posteriorly and is additionally separated from the main cochlear cavity by a thin but definitive tectorial membrane, which arises from the inferior margin of the limbic lip and extends to contact the basilar papilla.

The entire lateral surface of the limbus and basilar membrane and the surfaces of the limbic lip are covered with an epithelium continuous with that lining the entire cochlear duct. This layer is low and cuboidal except where it is specialized to form the basilar papilla in the central region of the basilar membrane, and at the limbic lip where it gives rise to the tectorial membrane.

The basilar papilla is fusiform and comprises 23 percent of the sacculo-cochlear sensory area. In *Coleonyx* the papilla is elongate antero-posteriorly and extends posteriorly beyond the limits of both limbic hiatus and limbic lip. Here it rests upon the body of the limbus and not on the basilar membrane. Immediately adjacent to the anterior extremity of the basilar papilla is found the posterior limit of the short medial limb of the lagenar macula. The macula curves around the anterior and onto the lateral wall of the lagenar portion of the cochlear duct; here it expands vertically to reach its greatest dimension. The lateral limb is approximately as long as the medial. The entire macula constitutes approximately 60 percent of the sacculo-cochlear sensory area.

The sensory areas of the saccule and cochlear duct transmit impulses to the brain stem by way of the eighth cranial nerve. Fibers arise from the saccular macula and, traversing a distinct periotic channel, course inferomedially through the dense periotic connective tissue to the ganglionic cells located in the internal acoustic foramen. The ganglionic cells of the fibers supplying the lagenar macula are also located here. The lagenar ramuli course around the anterior edge of the cochlear duct within the periotic connective tissue and pick up fila from lateral to medial. The ganglionic cells of the fibers supplying the basilar papilla are located in a medial excavation of the limbus. The central fibers from all ganglionic cells course medially to exit from the otic capsule as a bundle comprising the eighth cranial nerve.

Situated posteriorly in the cochlear recess, between the footplate of the columella auris and the vestibular membrane, is the lower part of the periotic cistern. The cistern also extends superiorly and enters the vestibule to fill the cavity lateral to the saccule. This extension reaches anteriorly and posteriorly in the vestibule beyond the limits of the saccule. The anterior portion of the saccular part of the cistern is limited inferiorly by the cisternal septum and inferior cisternal crest. The superior cisternal crest, and saccular attachments thereto, limit the cistern superomedially. Projecting anteroinferiorly as a direct continuation of the lower part of the periotic cistern is the scala vestibuli. This channel, limited superiorly by the cisternal septum and inferior cisternal crest, projects anteriorly between the wall of the cochlear recess and the vestibular membrane. Anteriorly, approximately at the level of the anterior limit of the limbic lip, it sinks into a deep groove in the lateral bony wall. At the level of the anterior margin of the cochlear duct, the groove is closed to form a bony canal which houses the extension of the scala vestibuli, the helicotrema. The latter curves around the anterior wall of the cochlear duct, inclining inferiorly at an angle of approximately 45 degrees. Here, at the anterior limit of the cochlear duct, the bony canal gives way to a groove, and the helicotrema continues into the scala tympani.

Two well-defined periotic diverticula arise from the scala vestibuli. One, the scala lagenae, extends anteroinferiorly in direct relation to the lateral, expanded limb of the lagenar macula, then hooks medially under the lagenar part of the cochlear duct. Another, arising from the posterosuperior part of the scala vestibuli as a small, poorly-defined extension, courses between the cochlear duct and saccule and expands to form the scala sacculi in relation to the base of the saccular macula. The extension is easily followed anteriorly to the limit of the macula; due to disruption of tissue, I am not certain of the extent, if any, of its posterior expansion.

The scala tympani continues from the helicotrema as a definitive channel housed, for a short distance, in a groove in the medial wall of the cochlear recess. Medially, it is here related to the medial limb of the lagenar macula. Posterior to the macula and inferior to the cochlear ganglion, the scala tympani expands and terminates in the periotic sac, which is in relation to the basilar papilla and the anterior part of the limbus. A short, but definitive, accessory scala tympani extends posterosuperiorly in a groove in the lateral surface of the limbus and is related to the posterior part of the basilar membrane and papilla. The periotic sac extends slightly out of the otic capsule, through the periotic foramen, into the superomedial part of the recessus scalae tympani. Here, it is limited inferolaterally by the secondary tympanic membrane, which faces into the lateral part of the recessus scalae tympani that appears as a pit in the medial wall of the tympanic cavity. Medially, the periotic sac contains the meninges by way of the medial aperture of the recessus scalae tympani.

Sphaerodactylidae

(Figs. 4-9)

Underwood (1954) proposes a new family, the Sphaerodactylidae, that includes five genera. Of these, representatives of three genera (*Gonatodes*, *Sphaerodactylus* and *Lepidoblepharis*) were available for study. In contrast to the rather ubiquitous Eublepharidae, this family, as Underwood (*ibid.*) has proposed it, is restricted to the New World and is distributed "on the islands and continent surrounding the Caribbean Sea."

The lateral wall of the vestibule in *Sphaerodactylus* and *Lepidoblepharis* is regular and laterally concave; in *Gonatodes* it is irregular and is marked by ridges formed by the horizontal and vertical semicircular canals. In all three genera, the concavity of the lateral wall is more angular than in either species of *Coleonyx* examined, and properly could be divided into superior and inferior portions at the level of the horizontal semicircular canal. The superior portion is directed superomedially and continues into the base of the superior cisternal crest; the inferior portion inclines toward, and continues into, the base of the inferior cisternal crest.

The inferior cisternal crest is directed superomedially toward the inferior margin of the saccule. In *Sphaerodactylus* and *Gonatodes* the crest is strongly developed and forms a distinct superior bony wall to the lateral part of the scala vestibuli; it extends posterior to the footplate of the columella auris and, here, forms the superior wall of a short diverticulum of the periotic cistern related to the lateral surface of the posterior ampullary area. In *Lepidoblepharis*, the inferior cisternal crest is little more than a slight ridge posteriorly, but anteriorly it is strongly developed in relation to the scala vestibuli. In the sphaerodactylids, this crest does not end posteriorly by blending into the lateral wall of the otic capsule, but forms a part of the wall of the recess for the posterior otic and periotic ampullae. Anteriorly, it enters into the formation of the floor of the anterior portion of the vestibule and the roof of the lagenar portion of the cochlear recess.

The superior cisternal crest, in *Sphaerodactylus* and *Lepidoblepharis*, is prominent and clearly demarcated; in *Gonatodes* it is no more than a slight elevation on the superolateral wall of the vestibule adjacent to the superior margin of the saccule.

The anterior portion of the medial vestibular wall, in relation to the common crus, is medially concave. Posteriorly, the wall tends to flatten, as in *Coleonyx,* and slant medially in all of the genera except *Sphaerodactylus,* in which the posterior part is bulged by the prominence of the recess for the posterior ampulla. In the anterior superior quadrant of the medial wall, the vestibular aqueduct courses superiorly to communicate with the cranial vault. Inferior to this opening, in the floor of the vestibule, a foramen affords exit to the fibers of the eighth cranial nerve which arise from the sensory areas located here.

The cochlear recess in the Sphaerodactylidae is similar to that found in *Coleonyx;* in *Gonatodes,* however, it is shaped more like a rectangular solid than an inverted pyramid. In all available representatives of the family, the cochlear recess is more clearly delimited from the vestibule than in *Coleonyx* because of the prominence of the inferior cisternal crest and a ridge opposite it on the medial wall. The oval window occupies a minor portion of the lateral wall of the cochlear recess and is filled by a comparatively-small oval footplate of the columella auris. In these genera, the short shaft of the columella is not eccentrically attached to the footplate, but is centrally placed.

The medial wall of the cochlear recess is somewhat variable and complicated in the Sphaerodactylidae. In *Gonatodes* (as in *Cole-*

onyx) the anterior margin of the periotic foramen is situated opposite the anterior margin of the footplate of the columella and extends posteriorly to the level of the columellar shaft. In *Lepidoblepharis* the anterior limit of the periotic foramen is shifted posteriorly, relative to the columella, and is situated at the level of the columellar shaft; its posterior margin lies opposite the posterior limit of the oval window. In *Sphaerodactylus* the foramen is located entirely caudal to the level of the columella auris, just anterior to the posterior limit of the cochlear recess. The size of the recessus scalae tympani, into which the periotic foramen opens, varies from rather small in *Sphaerodactylus* to large in *Lepidoblepharis.* In all three genera the medial aperture of the recessus scalae tympani varies in size directly with the size of the recessus. The medial aperture is not divided by a strut like that found in *Coleonyx,* but does afford passage to the fibers of the ninth cranial nerve. The lateral aperture is closed by the secondary tympanic membrane and faces inferolaterally directly into the tympanic cavity; thus, no distinct pit is present in the medial wall of the tympanic cavity in these forms.

The fibers of the eighth cranial nerve exit from the otic cavity by way of three openings. Anteriorly, generally in close relationship to the seventh cranial nerve, a few fibers pass through the anterior acoustic foramen from the sensory areas of the lateral and anterior ampullae. At the level of the vestibular aquaeduct, the posterior ramus of the eighth cranial nerve exits through the posterior acoustic foramen. This opening is divided horizontally in these genera, hence the posterior ramus is formed from superior and inferior divisions. The inferior division ascends from the sensory areas of the cochlear duct; superiorly, fibers exit from the vestibule from the sensory areas of the saccule, utricle and posterior ampulla.

From its lateral aspect, the saccule is rather uniformly rectangular. It is antero-posteriorly compressed, and gives the impression of vertical elongation. The medial saccular wall is medially concave and is affixed by a deposition of periotic connective tissue heavier in these lizards than in *Coleonyx.* At approximately the level of the common crus, the otic duct empties into the saccule at its dorsal margin; just posterior to this the sacculo-utricular duct is found. The saccular epithelium is low cuboidal and, in the lower half of the medial wall, is specialized to form the hair cells of the saccular macula. The shape of the macula is somewhat different in each of the three genera. In *Gonatodes* it is like an hour-glass with a distinct constriction just anterior to its mid-point; in *Lepidoblepharis* the constriction is present, but not as marked, and the macula is smaller anteriorly than posteriorly. The saccular macula in *Sphaerodactylus* is oval and lacks the constriction present in representatives of the other two genera.

The lateral saccular wall in these sphaerodactylids appears to be heavier than that in *Coleonyx* because of relatively more periotic connective tissue being deposited around the epithelium. A large granular mass of connective tissue is associated with the lateral wall of the saccule in all three genera; in *Sphaerodactylus* this appears to be fused with the lateral wall of the vestibule. In both *Sphaerodactylus* and *Lepidoblepharis* it is dense, darkly staining and highly organized, whereas, in *Gonatodes*, it stains lightly and is somewhat diffuse.

The saccule tapers into the sacculo-cochlear duct, which arises as a short extension of the posteroinferior angle of the saccule. The duct is not clearly defined, but blends almost insensibly into the structure of the saccule and cochlear duct. The cochlear duct itself is roughly pyramidal, antero-posteriorly shortened and, in all of the Sphaerodactylidae examined, bends laterally to follow the general contour of the medial wall of the cochlear recess. The vestibular membrane is well defined and (as in *Coleonyx*) is of the same relative thickness as the lateral saccular wall. Superiorly, the membrane is continuous with a definitive superolateral portion of the wall of the cochlear duct. This part of the wall lies opposite the inferior part of the medial wall of the saccule in the area of the saccular macula. A thin layer of periotic connective tissue intervenes between, and fuses with, the opposing membranes, thus uniting the layers into a single, rather thick wall which separates the cavity of the saccule from that of the cochlear duct.

The limbus is prominent in both *Lepidoblepharis* and *Gonatodes,* but, relative to the size of the cochlear duct, it is smaller than in *Coleonyx.* The limbus of *Sphaerodactylus* is large and is related to most of the medial wall of the cochlear duct. In all three genera, the limbus begins just anterior to the sacculo-cochlear duct, high on the medial wall and proximate to the medial wall of the saccule. It is composed of the same type of dense, highly organized periotic connective tissue found in other lizards. The body of the limbus in *Gonatodes* is larger than that found in *Lepidoblepharis* (where it is rather delicate and small) and has a large, inferiorly-curving limbic lip which overhangs the basilar papilla and forms a deep cochlear sulcus with the body of the limbus. The limbic lip in

Lepidoblepharis is small, does not overhang the basilar papilla, and forms a shallow cochlear sulcus. A well-defined tectorial membrane extends from the tip of the limbic lip in both genera and rests upon the hair cells of the basilar papilla. The limbic lip in *Sphaerodactylus* is less prominent than in the other two genera. It appears as a diffuse, lightly-stained addendum projecting laterally from the dorsal part of the body of the limbus; because it curves only slightly inferiorly, it does not form a definitive cochlear sulcus. In the specimen available, no tectorial membrane could be discerned, but might have been absent due to loss during preparation.

Posteriorly, the basilar papilla rests upon the basilar membrane stretched across the limbic hiatus, and lies directly opposite the footplate of the columella. The papilla extends posteriorly and overrides the body of the limbus. In *Sphaerodactylus* this condition is exaggerated and the papilla extends significantly into the cochlear sulcus. In *Lepidoblepharis,* at the other extreme, the overlap is barely apparent. The shape of the papilla varies within the group; in *Gonatodes* it is fusiform, in *Lepidoblepharis* it approaches the shape of an equilateral triangle, and in *Sphaerodactylus* it is somewhat vertically oriented and oval. The lagenar macula extends craniad along the cochlear wall immediately anterior to the basilar papilla. At the anterior limit of the cochlear duct it turns laterally and dorsally to cross the anterior margin of the cochlear duct and pass posteriorly and superiorly on the lateral wall of the cochlear duct. The lateral part of the macula is generally more vertically expanded than the medial, and, because of its dorsal orientation, is usually higher than the medial. In *Lepidoblepharis* the anterior, curved part of the macula is narrow, but in the other two genera the anterior part expresses a continuation of the general vertical expansion that takes place from medial to lateral.

The size of the basilar papilla remains relatively constant within the three genera, varying only from 10 percent in *Lepidoblepharis* to 16 percent in *Sphaerodactylus* and 17 percent in *Gonatodes.* The lagenar macula varies inversely in size with the saccular macula; in *Sphaerodactylus* there is an approximate 1:1 relationship (lagenar macula—44 percent; saccular macula—40 percent) although the lagenar macula is larger than the saccular macula. In *Lepidoblepharis* the lagenar macula is smaller than the saccular macula (43 percent:47 percent, respectively), and in *Gonatodes* the lagenar macula is much larger than the saccular macula (66 percent:17 percent, respectively).

For the most part, the main periotic channels in the Sphaerodactylidae are not unlike those of other lizards; there are specific modifications, however, that are of particular importance. Generally, the periotic cistern is in relation to the lateral wall of the cochlear duct and, superiorly, is located within the lateral portion of the vestibule in relation to the lateral saccular wall. It extends beyond the limits of the saccule both anteriorly and posteriorly. The superior cisternal extension connects with the inferior, cochlear, portion of the cistern more anteriorly than in *Coleonyx;* posteriorly it is separated from the cochlear portion of the cistern by the prominent inferior cisternal crest, and, anterior to this connection, by this crest and a cisternal septum. The scala vestibuli extends as an anteroinferior projection of the cistern to end in the helicotrema. A scala lagenae, well defined in *Lepidoblepharis,* arises from the scala vestibuli and, coursing inferiorly and somewhat anteriorly, hooks inferomedially for some distance under the lagenar portion of the cochlear duct; it is poorly defined, or absent, in *Gonatodes* and *Sphaerodactylus.* In *Lepidoblepharis* and *Gonatodes* the posteromedial portion of the helicotrema is housed in a bony depression in the otic capsule; in *Sphaerodactylus,* this portion of the channel dips into the periotic connective tissue surrounding the walls of the cochlear duct. The helicotrema is continued into the short, expanded periotic sac which extends slightly through the periotic foramen into the recessus scalae tympani and helps form the inferolaterally-directed secondary tympanic membrane. This membrane is attached toward the periphery of the recessus scalae tympani and this attachment, in effect, reduces the size of the unoccupied part of the recess.

As far as can be determined from the material available, there is no scala sacculi present in these sphaerodactylids. There is some indication of an extremely small periotic space in relation to the saccular macula, but its connection with the main periotic channels is either extremely small or non-existent. An accessory scala tympani is not present in any of the forms examined, and probably is absent within the Family Sphaerodactylidae.

Gekkonidae

(Figs. 10-24, 27)

The Gekkonidae are the most widespread of the gekkonoid lizards. Underwood (1954) includes approximately 60 genera within the family; of these, 22 genera are listed under the Subfamily

Diplodactylinae, and 38 genera under the Subfamily Gekkoninae. Five genera were available for this study, three of the Gekkoninae and two of the Diplodactylinae.

The lateral wall of the vestibule shows varying degrees of concavity in the Gekkonidae; in *Thecadactylus* the wall is markedly concave, whereas, in *Phyllodactylus, Hemidactylus* and *Aristelliger* the curvature of the lateral wall resembles that found in *Coleonyx*. In *Gymnodactylus* little or no concavity is present in the wall; here it is rather straight, smooth and terminates superiorly and inferiorly in the superior and inferior cisternal crests, respectively. The inferior cisternal crest is distinct in all of the gekkonids examined; in some genera, such as *Aristelliger*, it is directed sharply superiorly, but in others (*Phyllodactylus, Hemidactylus*) this is less apparent. It begins at the posterior limit of the vestibule as a small, superiorly-directed ridge that is an extension of the posterolateral portion of the floor of the vestibule. Anteriorly, it widens medially and shows a slight inferior bow as it becomes the superior wall of the depression housing the scala vestibuli; anteriorly, it also becomes thin and delicate. Just short of the anterior limit of the vestibule, the inferior cisternal crest fuses with a protrusion from the medial wall to form the anterior bony floor of the vestibule and the roof of the lagenar portion of the cochlear recess.

The superior cisternal crest begins as a small ridge posterosuperior to the footplate of the columella and continues anteriorly as a distinct line of saccular attachment of constant size in *Gymnodactylus, Phyllodactylus* and *Hemidactylus*. In *Thecadactylus* it is prominent anteriorly but less so posteriorly. In the genera mentioned above, the superior cisternal crest is larger than in representatives of the other families examined; in *Aristelliger* it is, however, rather poorly defined throughout its length.

The medial wall of the vestibule is medially concave throughout its entire antero-posterior length. The evenness of the concavity is broken at various points by ridges and, just anterior to the midpoint of the vestibule, by the vestibular aquaeduct, which courses superiorly to provide communication with the cranial cavity.

The structure of the gekkonid cochlear recess is essentially similar to that of *Coleonyx*, but differs from the basic pattern noted in the sphaerodactylids. The oval window is longitudinally elongated, as is the footplate of the columella auris. The columellar shaft is eccentrically attached to the footplate just anterior to its posterior margin. Except in *Gymnodactylus*, the periotic foramen is located directly opposite the major expanse of the footplate; it begins at the level of the anterior limit of the footplate and extends posteriorly approximately to the level of the shaft of the columella auris. In *Gymnodactylus* the periotic foramen is situated opposite the point of attachment of the shaft to the footplate. The foramen opens into a uniformly large recessus scalae tympani, grossly visible in sectioned material. The medial aperture of the recess is divided into two portions by a strong strut of bone oriented so that the posterior opening is superior to the anterior. The former provides exit from the cranial cavity for fibers of the ninth cranial nerve; both parts of the aperture are closed by meninges and periotic tissue. The lateral aperture of the recessus scalae tympani faces laterally directly into the tympanic cavity. The anterior and posterior acoustic foramina provide exit for fibers of the eighth cranial nerve from the otic capsule; the fibers coursing through the former arise from the anterior and lateral ampullae and those traversing the latter arise from the sensory areas of the cochlear recess and vestibule.

The shape of the saccule in the different gekkonid genera is somewhat variable; in *Phyllodactylus* it is an obliquely-placed ovoid structure which closely resembles that found in *Coleonyx,* whereas, in *Gymnodactylus,* it is similar to that found in the three sphaerodactylid genera. When viewed from the lateral aspect, the saccule in *Hemidactylus, Thecadactylus* and *Aristelliger* is an elongate rectangle. The medial saccular wall, in all of the gekkonid genera examined, is well defined and has around it a distinct thick deposition of periotic connective tissue, which the otic and sacculo-utricular ducts traverse before becoming continuous with the saccular cavity. The lining epithelium of the wall, as in other forms, is cuboidal and is specialized inferiorly to form a saccular macula that assumes one of two shapes: In *Hemidactylus, Phyllodactylus* and *Gymnodactylus* it is an oval that occupies most of the middle portion of the wall (in *Phyllodactylus* this oval is somewhat elongated); in *Thecadactylus* and *Aristelliger* the macula is centrally constricted (in the former, its anterior portion is vertically larger and more horizontally shortened than is its elongate posterior portion).

In *Hemidactylus* the lateral saccular wall is thin and poorly defined; the other four genera studied exhibit distinct lateral saccular walls with considerable periotic connective tissue deposited adjacent to them. In all genera except *Gymnodactylus,* the connective tissue mass which is differentiated within the membrana propria (identified previously in other gekkonoid genera), is conspicuous and, in some forms, appears to constrict the saccular cavity. In *Gymnodactylus* this inclusion is diffuse, lightly stained and similar to that in the sphaerodactylid *Gonatodes.* The saccule is invariably attached superiorly to the superior cisternal crest. In some instances the intervention of a cisternal septum between the inferior saccular margin and the inferior cisternal crest is replaced by direct contact of the saccule with the crest; this latter situation is found in *Aristelliger, Phyllodactylus* and *Gymnodactylus.*

The sacculo-cochlear duct is distinct in the gekkonids, although there is some variation in its morphology. In *Hemidactylus, Gymnodactylus* and *Phyllodactylus* it assumes the vertical cylindrical shape found in many other reptilian genera; it arises from the posterior aspect of the saccular wall and terminates in the most posterior portion of the cochlear duct. In *Thecadactylus* and *Aristelliger,* however, it arises from the medially wall of the saccule as an antero-posteriorly broad channel and extends somewhat posteriorly and inferiorly to terminate in the posterior portion of the superior wall of the cochlear duct.

The cochlear duct, in which the sacculo-cochlear duct terminates, is usually pyramidal in the gekkonids examined. There are certain subtle differences in size, both relative and real, that are of interest, but there are only two points of apparent significance concerning the gross morphology of the sacculo-cochlear complex. In all genera except *Aristelliger* and *Thecadactylus,* the cochlear duct has a slight curvature directed laterally away from the medial wall of the cochlear recess; in the latter, the curvature is medially directed. Secondly, in *Gymnodactylus,* the cochlear duct and saccule are antero-posteriorly shortened, much as those in the sphaerodactylids; in inner ear structure, this genus departs strongly from the majority of the gekkonids.

The cochlear duct is lined by low cuboidal epithelium which grades into neuroepithelial cells in the vicinity of the limbus and lagena. The epithelial cells rest upon a rather thick (especially anteriorly) condensation of periotic connective tissue that encircles the whole duct and thus forms a relatively thick lateral cochlear wall (vestibular membrane). In some forms, such as *Aristelliger, Phyllodactylus* and *Thecadactylus,* the periotic tissue is considerably denser than in either *Hemidactylus* or *Gymnodactylus;* in all of these gekkonids this connective tissue is more pronounced than in either of the other two families studied. The vestibular membrane contains a variable number of blood vessels embedded within the supportive connective tissue, yet, in each genus, remains essentially the same thickness as the lateral saccular wall. In *Gymnodactylus,* superior and inferior portions of the lateral wall of the cochlear duct may be recognized. The superior portion is related to the inferomedial saccular wall, but the continuity of the periotic connective tissue is interrupted by the scala sacculi. This relationship of adjacent walls of the saccule and cochlear duct is similar to that found in the sphaerodactylids, and, to a lesser degree, in *Hemidactylus* and other gekkonid genera.

The limbus is somewhat larger in the gekkonid genera than in the other genera studied. The limbus here, too, is composed of dense periotic connective tissue, and an extension from the superior border of the body (the long, delicate limbic lip) forms a deep cochlear sulcus limited inferiorly by a distinct and, usually, large tectorial membrane.

The basilar papilla rests upon a thick basilar membrane. In all five genera the papilla is attenuated posteriorly (as in *Coleonyx* and the sphaerodactylids), mounts upon the body of the limbus and extends almost into the lumen of the sacculo-cochlear duct. At its posterior extremity it is neither covered by the limbic lip nor does it have a tectorial membrane resting upon it. It is interesting to note that the papilla rests upon the basilar membrane at all times even though it is not directly over the limbic hiatus, for the membrane extends over and closes the groove in the limbic issue in which the accessory scala tympani is situated The papilla, antero-posteriorly lengthened, is shaped like a teardrop and, within the gekkonids, comprises from 17 percent to 41 percent of the total sacculo-cochlear sensory area.

The lagenar macula occupies portions of the medial, anterior and lateral walls of the cochlear duct. This macula is smallest in *Gymnodactylus;* in this form its greatest vertical expansion is on the medial wall of the cochlear duct and, teardrop-like, it extends only slightly around the anterior wall. *Phyllodactylus* and *Hemidactylus* possess maculae which extend considerably onto the lateral wall of the cochlear duct; in the former, the greatest vertical expansion is on the anterior wall, while in the latter, the macula is oval and expands vertically on the lateral wall. In both *Aristelliger* and *Thecadactylus,* an anterior constriction separates medial and lateral expanded parts of the macula. This sensory area occupies from 23 percent to 41 percent of the total auditory area in the gekkonids.

The periotic channels found in the gekkonids exhibit the same general pattern as those found in other gekkonoid lizards, except that, in some instances, certain aspects are more clearly defined. The vestibular membrane is laterally related to the periotic cistern and scala vestibuli. A large extension of the cistern lies superior to the inferior cisternal crest and lateral to the lateral saccular wall (saccular portion of the cistern) and communicates with the cistern proper only toward its posterior extent. Elsewhere, these two parts are separated either by an inferior cisternal crest, a cisternal septum, or both. The saccular portion may, in some forms (*Aristelliger* and *Thecadactylus*), extend over the superior margin of the saccule or around the anterior margin to come into limited relationship with the medial saccular wall. In instances where the saccular wall appears to attach to the wall of the vestibule, the periotic channel surrounds the point of attachment (*Hemidactylus* and *Sphaerodactylus*).

The cistern continues anteriorly into the inferomedially-directed scala vestibuli. This structure is limited superiorly by either an inferior cisternal crest or a cisternal septum; the crest provides an incomplete bony roof for the scala. The scala vestibuli is well defined, relatively large and terminates by emptying into the helicotrema. In all of the gekkonids examined, the scala vestibuli has two quite-distinct diverticula (present to a degree in *Coleonyx*, but either poorly defined or absent in the sphaerodactylids). A clearly-defined duct courses between the cochlear duct and saccule and expands (in relation to the saccular macula) into a "Y-shaped" scala sacculi. Inferiorly, an unciform scala lagenae comes into relationship with the portion of the lagenar macula located on the medial side of the cochlear duct.

The helicotrema curves inferomedially around the anterior limit of the cochlear duct, embedded in a channel of bone, at an angle of approximately 45 degrees. It terminates in a short scala tympani which, in turn, empties into the periotic sac in relationship to the basilar papilla. The scala tympani is directly related to the medial portion of the lagenar macula. The periotic sac is related to the basilar papilla at the limbic hiatus and gives rise to the accessory scala tympani, which extends posterosuperiorly in relationship to the posterior part of the basilar papilla. The periotic sac extends inferiorly into the recessus scalae tympani and contributes to the formation of the inferiorly-directed secondary tympanic membrane, which, in these genera, faces into a rather large lateral portion of the recessus scalae tympani that appears as a pit in the medial wall of the tympanic cavity. The sac also comes into relationship with the meningeal lining of the cranial cavity by way of the medial aperture of the recess.

DISCUSSION

The vestibule of the otic capsule exhibits little diversity within the genera studied. The lateral wall of the vestibule is decidedly laterally concave in all forms except *Gymnodactylus;* it ends inferiorly in a well-defined inferior cisternal crest and superiorly in a (sometimes) well-defined superior cisternal crest. In the sphaerodactylids the lateral wall is more angular than in either of the other two families; this character is distinctive and has been noted only in the Family Sphaerodactylidae. The inferior cisternal crest is better demarcated in the gekkonoids than in most other lizards and, for the most part, provides a clear distinction between the vestibule and the cochlear recess; in *Coleonyx,* where the crest is somewhat smaller, this division is not as apparent as in other gekkonoids. The medial wall of the vestibule is noteworthy in its relative lack of diversity. In all of the genera studied the various formamina were regular in their position in the wall.

In the cochlear recess more significant morphological differences emerge. The differentiation here between the gekkonids and *Coleonyx* is slight, but the sphaerodactylids show certain structural modifications that clearly set them off as a distinct unit. The cochlear recess in all gekkonoid genera is generally pyramidal in shape and has a variably-defined lagenar recess. Other than the periotic foramen, the medial wall of the cochlear recess generally has one opening that provides exit for the fibers of the eighth cranial nerve; in the sphaerodactylids this posterior acoustic foramen is divided by a horizontal strut of bone into two openings, a superior one which serves the fibers coming from the vestibule, and an inferior one which serves the fibers coming from the cochlear recess.

A particularly important relationship within the cochlear recess concerns the position of the columella auris relative to the periotic foramen in the medial wall of the recess. In *Coleonyx* the shaft of the columella is attached toward the posterior portion of the footplate and the periotic foramen lies directly opposite the anterior, larger, part of the footplate. Essentially the same condition is found in the gekkonid *Phyllodactylus.* In all of the gekkonid genera except *Gymnodactylus*, the foramen similarly opens opposite the anterior portion of the footplate; in these genera, also, the shaft of the columella joins the footplate distinctly posterior to its mid-point. In *Gymnodactylus* the periotic foramen opens opposite the attachment of the shaft, more posteriorly than in the other gekkonids. The position of the periotic foramen relative to the footplate of the columella in *Gonatodes* closely parallels the condition found in *Coleonyx* and the majority of gekkonids. The shaft of the columella, however, attaches near the center of the footplate, a character found in all of the sphaerodactylids. In *Lepidoblepharis* the foramen opens posterior to the centrally-placed shaft, and in *Sphaerodactylus* it opens posterior to the entire footplate.

It is thus apparent that, in the gekkonids, the shaft of the columella auris regularly joins the footplate eccentrically, and the periotic foramen (except in *Gymnodactylus*) opens opposite the anterior portion of the footplate. In the sphaerodactylus a posterior migration of the periotic foramen relative to the footplate is apparent in the three genera examined, and the shaft of the columella is centrally placed. Too small a sampling of the eublepharids was utilized to make any significant generalizations, other than those made specifically for the one genus, *Coleonyx*.

An interesting structure, highly developed and common to all gekkonoids, is the pit into which the secondary tympanic membrane faces. According to Baird (1960) this structure is found in other primitive lizards and would seem, in itself, to be a primitive feature. There seems to be no real difference in this structure from family to family within the gekkonoids, other than in the degree of its expression. Here again, the sphaerodactylids can be separated easily from the genera of the other families, for in this group the size of the pit is considerably reduced, and the secondary tympanic membrane faces more laterally than inferiorly (except in *Gonatodes*). This character suggests that the sphaerodactylids are, relatively, not an old assemblage. *Gonatodes* has a rather well-defined pit, and, on the basis of this character, might be interpreted as representing a more primitive type of sphaerodactylid.

Although the shape of the saccule varies within families and shows some interfamilial overlap, certain clear-cut morphological patterns can be detected within the Superfamily Gekkonoidea. The saccule in the sphaerodactylids shows decided differences from that in other genera in that it is horizontally shortened and vertically lengthened. *Gymnodactylus*, a gekkonid, also has this feature, one of many characters common to it and the sphaerodactylids. In

Coleonyx, the small, obliquely-placed saccule is rather distinctive and is different from that of the sphaerodactylids and the majority of the gekkonids studied; *Phyllodactylus,* however, does have a saccule of similar shape. Other than *Phyllodactylus,* the gekkonids generally have a rectangular saccule of approximately equal vertical and horizontal dimensions. The walls of the saccule in all genera are supported by varying amounts of periotic connective tissue that seems to show some family specificity. In *Coleonyx* there appears to be less of this connective tissue than is found in the sphaerodactylids; in the latter there is less than in the gekkonids.

The otolith-like mass present laterally in the saccule is of some interest, more because of lack of understanding than of knowledge about it. From the sections available for this study, it was determined that the mass is an elaboration of the membrana propria immediately external to the epithelium of the central region of the lateral saccular wall. The mass contains regular, deep-staining granules (except in *Gonatodes* and *Gymnodactylus* where the granules stain lightly and diffusely) in a conglomerate situated directly opposite the saccular macula. It was thought, at first, that these were free granules within the saccular cavity, and that they acted in the capacity of an accessory to the otolith of the saccular sensory area. On closer observation, it was determined that the granules are not free, but are, indeed, contained within periotic tissue of the lateral saccular wall. From comparison with stained granules in the otic sac, it was determined that these granules are not particularly similar to the general calcium deposits found within the labyrinth; they have some staining properties similar to bone, but do not show any of the histological characteristics of bone. In most of the gekkonoids examined, this mass was large and clearly defined; its size in other lizards, on subjective evaluation, is less than in gekkonoids.

The sacculo-cochlear duct shows some rather distinct modifications, not only within the families, but from genus to genus; not all morphological types can be family-oriented, however. In the majority of lizards, this structure is a cylindrical tube arising from the posterior margin of the saccule and terminating in the postero-superior aspect of the cochlear duct. This general scheme is relatively consistent, and is especially evident in *Coleonyx* and the gekkonids, other than *Aristelliger* and *Thecadactylus.* The sphaerodactylids possess a unique variation of this; the duct blends with the saccule and cochlear duct and is almost indistinguishable from either. The only means by which the duct can be grossly defined in these forms is by artibrary statement that the posterior-most portion of the sacculo-cochlear complex constitutes the duct. Rather than arising posteriorly from the margin of the saccule, as it does in most lizards and in the genera cited above, in *Aristelliger* and *Thecadactylus* the sacculo-cochlear duct is quite distinctive; it comes off the posteroinferior aspect of the medial wall of the saccule as a rather broad channel that terminates in the posterosuperior margin of the cochlear duct. This situation is similar to that found in the primitive lizard *Sphenodon.*

It is in the cochlear duct that the most significant modifications are observed, not only with respect to gekkonoids alone, but with respect to the whole of the Reptilia. Phylogenetically, the cochlear duct occurs as an outpocketing of the saccule and, as such, is relatively more recently evolved than the saccule and the structures located in the vestibule. In the gekkonoid lizards this structure, in cross-section, is uniformly pyramidal with its apex directed anteroinferiorly. Regarded from the lateral or medial aspect, the cochlear duct resembles a well-defined rectangle. The gross shape of the structure varies from genus to genus, but, in the case of the sphaerodactylids, presents a form which exhibits some specific characteristics noted only in that family. In the latter family the cochlear duct is antero-posteriorly shortened, as is the saccule, and is vertically elongated so that the rectangular duct has its long axis oriented vertically. In the other families the cochlear duct is approximately as long as it is tall (in reality, the antero-posterior horizontal axis is slightly longer than the vertical axis). One form, *Gymnodactylus,* diverges from the normal gekkonid condition and has a cochlear duct grossly similar to that of the sphaerodactylids.

The unique form of the limbus constitutes the greatest modification observable in the sacculo-cochlear complex and is relatively well restricted to the families of the gekkonoids and pygopodoids. Shute and Bellairs (1953) were apparently the first investigators to describe the gekkonoid limbus and limbic lip in any detail, and were the first to note the resemblance of these structures to those of pygopodoids. As mentioned previously, however, de Burlet (1934) did define and name the limbic lip (labium vestibuli) in a specimen of *Gecko.* Its obvious divergence from the usual limbic form apparently did not impress him, and, although his term is applicable and probably holds precedence, the term limbic lip seems more descriptive and appropriate.

The morphology of the limbus changes little from family to family. In all, the size of the limbus is relatively constant. The large overhanging lip provides a point of origin for the tectorial membrane, and at no time does the lip overhang or rest upon the basilar papilla. The cochlear sulcus, formed by the limbic lip and bounded inferiorly by the tectorial membrane, encloses a certain amount of otic fluid and forms an anteroinferiorly-directed channel within the cochlear duct; this channel communicates with the main cavity of the cochlear duct (1) posterosuperiorly, adjacent to the orifice of the sacculo-cochlear duct, and (2) anteroinferiorly, adjacent to the lagenar macula. This channel is largest anteriorly in the region in which the basilar papilla is located. The papilla extends posterosuperiorly somewhat beyond the limits of the sulcus and limbic lip in all gekkonoid genera. It appears that the tectorial membrane rests upon the neuroepithelial cells of the papilla, and that the greater part of these sensory cells is situated in a direct line between the fenestra ovalis in the lateral cochlear wall and the periotic foramen in the medial cochlear wall.

The limbus is composed of highly organized periotic connective tissue that achieves its greatest density in the area immediately surrounding the margin of the limbic hiatus. This is apparent through differential staining of the cells in that area. The tissue of the limbic lip and periphery of the limbus is not as dense and, presumably, therefore, is less rigid than the denser connective tissue at the limbic hiatus. The rigidity in the vicinity of the limbic hiatus can probably be attributed to the function of support of the basilar membrane.

In none of the sectioned material used here was the limbus seen to be directly applied to the medial wall of the cochlear recess. In the areas in which they are located, the inferior ganglia of the eighth cranial nerve intervened or, in the portions of the limbus not associated with these ganglia, the limbus was separated from the wall by loose periotic connective tissue. Probably in unfixed specimens the limbus is attached to the cochlear wall by this loose connective tissue and, in life, possibly is relatively unstable; Shute and Bellairs (1953) suggest that its position is maintained by intraotic pressure in living animals.

The lagena is barely discernable grossly as a definitive structure of the otic system. It houses at least part of the macula lagenae, the sensory area associated with the anterior part of the cochlear duct. This sensory area is close to, and at times nearly touches, the anterior extremity of the basilar papilla and, in these lizards, usually curves anteriorly and laterally to occupy, variously, portions of the anterior and lateral walls of the cochlear duct. The cells of the macula rest upon an anterior extension of the same periotic connective tissue that composes the limbus and wraps around and supports the anterior border of the cochlear duct. The lagenar macula assumes rather varied patterns in the gekkonoids, none of which are particularly meaningful or fit into any pattern trend. The sphaerodactylids do show a tendency toward an anterior constriction of the macula that continues into an expansion on the lateral wall of the cochlear duct. The gekkonids do not apparently show any pattern in macular shape; *Thecadactylus* and *Aristelliger* show an expansion of the macula on the lateral wall of the cochlear duct and an interior construction similar to that of the sphaerodactylids. It is possible that the extension of the lagenar macula onto the anterior and lateral walls of the cochlear duct is typical of gekkonoids.

As is the case with other aspects of internal otic anatomy, the periotic system clearly shows differences delineating the sphaerodactylids from the other genera. All of the genera show a clearly-defined periotic cistern having a saccular extension that is separated from the main cistern and scala vestibuli by a cisternal septum and/or an inferior cisternal crest. In all forms, the scala vestibuli continues as an anterior extension of the periotic cistern and terminates in the helicotrema. The latter bends around the anterior aspect of the cochlear duct and descends at an angle of approximately 45 degrees, generally embedded in a bony canal in the anterior wall of the cochlear recess. The helicotrema ends laterally in a short scala tympani, which empties into the periotic sac. This sac is an expanded fluid compartment related to the medial surface of the limbus and extends inferomedially into the recessus scalae tympani. In all genera except the sphaerodactylids, a scala sacculi and an accessory scala tympani are present and related to the saccular macula and to the posterior part of the basilar papilla, respectively. That they are not present in the sphaerodactylids supports the contention of Underwood (1954) that these genera may be isolated as a separate family.

As is suggested by Shute and Bellairs (1953), the inner ear does appear to be a relatively important and significant organ for taxonomic study; the data resulting from this study tend to support the taxonomic organization of gekkonoid lizards proposed by

Underwood (1954). Insufficient work has been done on the eublepharids to draw firm conclusions at this time; it appears, however, that the saccule and cochlear duct of *Coleonyx* assume shapes significantly different from those shown by the majority of other gekkonoids studied here. The morphological description given earlier, then, may be considered typical of *Coleonyx*, and, possibly, of other eublepharids. The morphological differences observed in the otic system of the Sphaerodactylidae surely set them apart from *Coleonyx* and the majority of the gekkonids. Horizontal shortening and vertical elongation of the sacculo-cochlear complex is typical of the Sphaerodactylidae. The gekkonids are less easily categorized, possibly because they are a less homogeneous group, as is indicated by Underwood's (1954) split of the family into two subfamiles. The otic morphology of one member of the gekkonids resembles that of *Coleonyx* and that of another resembles the sphaerodactylid condition. Until more is known about the otic morphology of the gekkonids, no typical organization can be postulated; possibly, after more specimens are studied, some rational order may be ascertained on the basis of morphological evidence from the inner ear.

The genera utilized here seem to be well chosen for phylogenetic study. Little doubt now exists concerning the antiquity of the Eublepharidae. Underwood (1954) considers the group to be an early off-shoot of the first definitive gekkonoid lizards. Convincing anatomical support is supplied by Noble (1921), who states that the hyoid apparatus in *Coleonyx* is the most primitive found among the lacertilians. The morphology of the sacculo-cochlear complex of this form is clearly conservative and retains the same general pattern exhibited by many lacertilians.

Morphologically, the sphaerodactylids depart strikingly from the conservative *Coleonyx*. The horizontally-shortened sacculo-cochlear complex and the relatively unidentifiable sacculo-cochlear duct appear to be relatively recent modifications. The reduction in the size of the recessus scalae tympani is probably, also, a recent modification. Although it does not depart greatly from the rest of the sphaerodactylids in most of its ear structures, *Gonatodes* does possess relationships of the secondary tympanic membrane which are essentially similar to those in the rest of the gekkonoids. Noble (1921) alludes to the fact that *Gonatodes* is relatively primitive and *Sphaerodactylus* relatively advanced, and, although his taxonomic grouping is not similar to the one suggested by Underwood (1954), he does group the sphaerodactylid genera utilized here as a morphogenetic unit. The position of the secondary tympanic membrane in *Gonatodes* is more primitive than that in the other sphaerodactylids, and the relationships of the columella auris and the periotic foramen in this genus approximate the condition found in *Coleonyx*. On the basis of this evidence, then, *Gonatodes* can be considered as representative of a primitive sphaerodactylid. There is a certain amount of confusion about sphaerodactylid relationships beyond *Gonatodes;* the conflict arises concerning the phylogenetic relationships of *Sphaerodactylus* and *Lepidoblepharis.* On the basis of osteology and digital formation, Noble (1921) places *Sphaerodactylus* in a position phylogenetically advanced from that occupied by *Lepidoblepharis;* evidence accumulated here on the posterior migration of the periotic foramen relative to the columella auris seems to support this contention. Conversely, however, there seems to be a trend in the development of sensory areas of the saccule and cochlear duct in the Sphaerodactylidae that indicates *Lepidoblepharis* is more advanced than is *Sphaerodactylus.*

Although the gekkonids are, for the most part, clearly separated from both *Coleonyx* and the sphaerodactylids, there are some morphological similarities between the families that can perhaps be partially explained on phylogenetic grounds. The shape of the sacculo-cochlear complex in *Phyllodactylus* closely parallels that in *Coleonyx;* this can be seen from the illustrations of the reconstructions of the saccule and cochlear duct (Figs. 2, 11). Noble (1921) also notes similarities in the skulls of these two lizards. The conservatism noted in the inner ear in *Phyllodactylus* and *Coleonyx,* coupled with other morphological similarities, tends to indicate that these lizards are representatives of a primitive type. Most of the other gekkonids do not exhibit this conservatism; in *Hemidactylus* the sacculo-cochlear complex is relatively horizontally elongated, whereas, in *Gymnodactylus,* this complex resembles that of the sphaerodactylids. The situation in *Aristelliger* and *Thecadactylus* is unique and will be considered later.

It is quite apparent that the structures of the inner ear could not have evolved orthogenetically in gekkonoid lizards, but probably arose in several distinct lines from the relatively simple structures of a common stock. Underwood (1954) proposes that these stock gekkonoids were "secretive although still diurnal." From this stock, the three conservative types, *Coleonyx, Gonatodes* and *Phyllodactylus,* probably arose; whether or not the limbus was modified in the primitive stock is debatable, although it seems improbable that this type of modification would arise independently at least three times.

The inner ear of *Phyllodactylus* is possibly representative of a type that may have given rise to that of definitive gekkonids. From this generalized type of structure, the horizontally elongated otic system found in *Hemidactylus* can easily be derived. It is equally possible to derive otic structures of *Gymnodactylus* from the same (phyllodactyloid) type by postulating slight antero-posterior shortening coupled with a rather unique and unpredictable increase in the size of the basilar papilla in relation to the other auditory sensory areas. Of the two distinct trends noted in the inner ear in gekkonids, the one found in *Gymnodactylus* is probably the more recent.

For the most part, morphology of the inner ear suggests that the sphaerodactylids are a recent group, probably derivable from the more conservative *Gonatodes.* The direction of the evolution of the inner ear within the group is not clear, but the bulk of evidence points toward a decided decrease in the size of the basilar papilla, probably associated with the loss of the voice; it is interesting to note that vocality has been reported in the majority of the other gekkonoid lizards (Underwood, 1954; Loveridge, 1947; and others).

Throughout this study it has become clear that there exists a definite similarity in the structure of the inner ears of *Aristelliger* and *Thecadactylus.* Reconstructions of portions of the otic systems of these lizards are similar in many respects, and, as indicated below, the sensory areas within the saccule and cochlear duct have essentially the same percentage sizes. The shape and placement of the sacculo-cochlear duct in these lizards is unique in the gekkonoid material studied. According to Baird (1960), the form and relationships of the duct are reminiscent of those found in the rhynchocephalian, *Sphenodon,* which, for all practical purposes, may be considered a primitive lizard. Resemblance of ear structures of *Aristelliger* to those of *Spenodon* is more or less understandable, for there are several aspects of the general anatomy of *Aristelliger* that point to its being a primitive gekkonoid (Underwood, 1954). *Thecadactylus,* however, does not appear to be primitive in its general anatomy and the similarities observed between its otic morphology and that of *Aristelliger* are difficult to explain in relation to other, perhaps more significant, anatomical characteristics. The form and relationships of the sacculo-cochlear duct and the positioning of the secondary tympanic membrane in *Aristelliger* and *Thecadactylus* seem to be primitive and would seem to attest to the antiquity of both of these animals, but until more is known about the phylogenetic and taxonomic relationships of *Thecadactylus* little more can be said about this convergence.

It is worthy of note that not all of the modifications mentioned above are applicable entirely to the gekkonoids. Boulenger (1885) places the gekkonoid lizards relatively close, taxonomically, to the pygopodoids. Camp (1923) widely separates the two groups on the basis of the presence or absence of the rectus superficialis muscle. In their article on the cochlear apparatus in these two groups, Shute and Bellairs (1953) note certain similarities in structure of the inner ear. Underwood (1957) further notes that there are many aspects of anatomy in which the groups exhibit similarities. Although, superficially, they do appear to be widely divergent (*i. e.*, the pygopodoids tend toward reduction of the limbs, assumption of fossorial habits and are restricted entirely to the continent of Australia; the gekkonoids are of widespread tropical and subtropical distribution and possess two distinct pairs of limbs), work of Underwood (*ibid.*) and Shute and Bellairs (*ibid.*) seems to support Boulenger's (*ibid.*) original contention.

Not only does the work of Shute and Bellairs (*ibid.*) show that the pygopodoids exhibit modifications of the limbus that closely parallel those in gekkonoids, but investigation of the plates of these authors shows that a well-defined inferior cisternal crest is present in the pygopodoid *Delma fraseri*. This seems to offer additional support to the contention that the gekkonoids and the pygopodoids arose from a common stock and then diverged strongly, one group from the other.

The basilar papilla, in the gekkonoid genera used here, is generally elongated antero-posteriorly and, thus, a portion is not in relationship to the tectorial membrane. This, coupled with the probable effect of the cochlear sulcus on papillar function, indicates that the gekkonoids possibly have a relatively highly selective auditory receptor. The lagenar and saccular maculae in these forms are in definite relationship to periotic spaces and, possibly, function as nonanalytical receptors of sound waves that are propagated throughout the periotic fluid; perhaps the great size of these maculae in the gekkonoids has some significance. Little can be said at this time concerning the function of the maculae; there is some suggestion (de Burlet, 1929, 1934; Weston, 1939) that the saccular macula has some auditory function, and Baird (1960) states the lagenar macula maintains periotic relationships throughout the Reptilia and can be considered one member of an auditory triad composed of the two maculae and the basilar papilla. Some attention was given to these sensory areas in this study, and it was found that there existed a subtle, yet clear, delineation of phylogenetic relationships.

The total area of each receptor was determined, using an optical grid, and, in each animal, the total sacculo-cochlear sensory area was calculated by simple addition; the percentage of the total auditory area that each contributed was computed and used as a basis for comparison of the sensory areas in the forms considered. These data are undoubtedly too restricted to allow any broad generalizations; there are, however, certain things that stand out rather clearly.

In all of the genera studied, the relative size of the basilar papilla varies but little. The only significant deviations observed are a great increase in size of the papilla in *Gymnodactylus* and a tendency toward decrease in papillar size in the sphaerodactylids. The reduction in the size of the papilla found in the latter is possibly a recent modification, which corresponds to other modifications noted previously in this group. Enlargement of the basilar papilla in *Gymnodactylus* is difficult to explain; this divergence is not toward the sphaerodactylids as are other modifications, but, in this respect, the ear seems to have developed independently. Within certain limits, the percentage of the entire sensory area contributed by the saccular macula and lagenar macula vary inversely; the saccular macula is generally slightly smaller than the lagenar macula. The development of the basilar papilla seems to be independent of the other two individual sensory areas, but does vary inversely when both maculae are considered as a unit.

As has been found in other aspects of otic morphology, a certain amount of correlation can be observed in the sensory areas in *Coleonyx, Gonatodes* and *Phyllodactylus;* in all three genera there is a relatively small saccular macula and a large lagenar macula. In all three instances, too, the basilar papilla is approximately the same size as the saccular macula. It would seem that a large lagenar macula may be a primitive characteristic.

It has been proposed on the basis of other evidence (see above) that *Aristelliger* is a primitive gekkonoid lizard. If *Coleonyx, Gonatodes* and *Phyllodactylus* posses a primitive arrangement of the sensory areas, then the sensory areas in *Aristelliger* (Fig. 26) diverge disturbingly from a primitive pattern. It seems entirely possible that this lizard is a representative of a primitive off-shoot, which has evolved its own pattern of ear morphology independent of other gekkonoids. The remaining gekkonoids studied here, on the other hand, can be placed into the same sort of phylogenetic pattern of sensory structures that was proposed on the basis of other characters of the inner ear.

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KEY TO ABBREVIATIONS

BL—body of the limbus.
BM—basilar membrane.
BP—basilar papilla.
CD—cochlear duct.
CS—cochlear sulcus.
FP—portion of the footplate of the columella auris.
G—ganglionic cells located in the excavation of the limbus.
GM—granular mass within the membrana propria of the lateral saccular wall.
ICC—inferior cisternal crest.
LL—limbic lip.
LPML—lateral portion of the macula lagenae.
ML—macula lagenae.
MPML—medial portion of the macula lagenae.
MS—macula sacculi.
PCSV—junction of the periotic cistern and scala vestibuli
PS—periotic sac.
S—saccule.
SC—saccular cavity.
SCC—superior cisternal crest.
SCD—sacculo-cochlear duct.
SCI—cisternal septum.
SPC—superior portion of the periotic cistern.
TM—tectorial membrane.
VM—vestibular membrane.

FIGURES 1-12

FIG. 1. View of the approximate position and extent of the medial parts of the sensory areas of the saccule and cochlear duct in *Coleonyx.* 16×

FIG. 2. Medial view of a reconstruction of the saccule and cochlear duct in *Coleonyx.* 16×

FIG. 3. View of the approximate position and extent of the lateral portion of the lagenar macula in *Coleonyx.* 16×

FIG. 4. View of the approximate position and extent of the medial parts of the sensory areas of the saccule and cochlear duct in *Sphaerodactylus.* 7×

FIG. 5. Medial view of a reconstruction of the saccule and cochlear duct in *Sphaerodactylus.* 7×

FIG. 6. View of the approximate position and extent of the lateral portion of the lagenar macula in *Sphaerodactylus.* 7×

FIG. 7. View of the approximate position and extent of the medial parts of the sensory areas of the saccule and cochlear duct in *Lepidoblepharis.* 14×

FIG. 8. Medial view of reconstruction of the saccule and cochlear duct in *Lepidolblepharis.* 14×

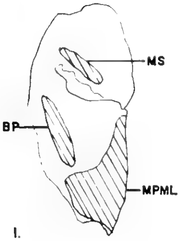
FIG. 9. View of the approximate position and extent of the lateral portion of the lagenar macula in *Lepidoblepharis.* 14×

FIG. 10. View of the approximate position and extent of the medial parts of the sensory areas of the saccule and cochlear duct in *Phyllodactylus.* 14×

FIG. 11. Medial view of a reconstruction of the saccule and cochlear duct in *Phyllodactylus.* 14×

FIG. 12. View of the approximate position and extent of the lateral portion of the lagenar macula in *Phyllodactylus.* 14×

Figures 1-12



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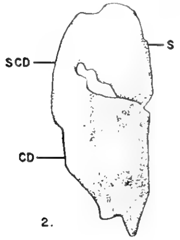

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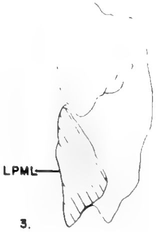

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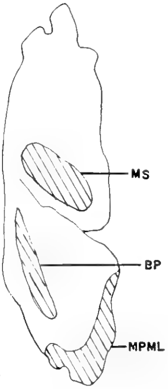

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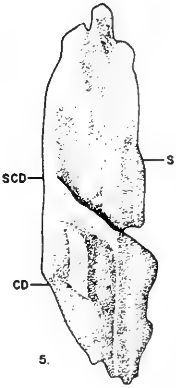

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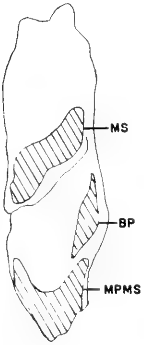

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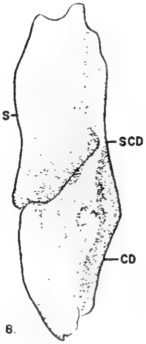

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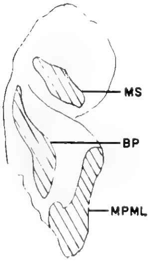

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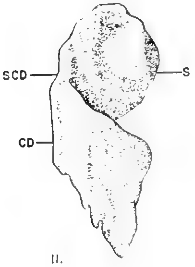

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FIGURES 13-24

FIG. 13. View of the approximate position and extent of the medial parts of the sensory areas of the saccule and cochlear duct in *Hemidactylus*. 14×

FIG. 14. Medial view of a reconstruction of the saccule and cochlear duct in *Hemidactylus*. 14×

FIG. 15. View of the approximate position and extent of the lateral portion of the lagenar macula in *Hemidactylus*. 14×

FIG. 16. View of the approximate position and extent of the medial parts of the sensory areas of the saccule and cochlear duct in *Aristelliger*. 14×

FIG. 17. Medial view of a reconstruction of the saccule and cochlear duct in *Aristelliger*. 14×

FIG. 18. View of the approximate position and extent of the lateral portion of the lagenar macula in *Aristelliger*. 14×

FIG. 19. View of the approximate position and extent of the medial parts of the sensory areas of the saccule and cochlear duct in *Thecadactylus*. 14×

FIG. 20. Medial view of a reconstruction of the saccule and cochlear duct in *Thecadactylus*. 14×

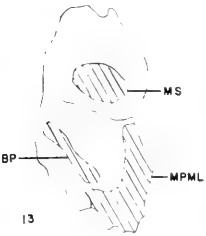
FIG. 21. View of the approximate position and extent of the lateral portion of the lagenar macula in *Thecadactylus*. 14×

FIG. 22. View of the approximate position and extent of the medial parts of the sensory areas of the saccule and cochlear duct in *Gymnodactylus*. 14×

FIG. 23. Medial view of a reconstruction of the saccule and cochlear duct in *Gymnodactylus*. 14×

FIG. 24. View of the approximate position and extent of the lateral portion of the lagenar macula in *Gymnodactylus*. 14×

FIGURES 13-24



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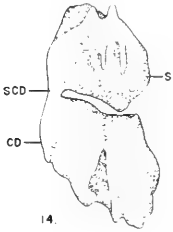

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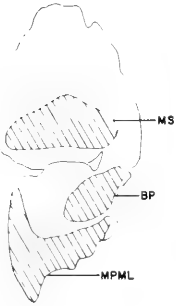

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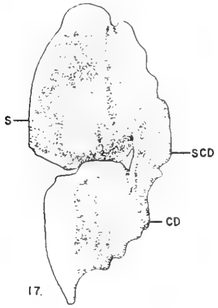

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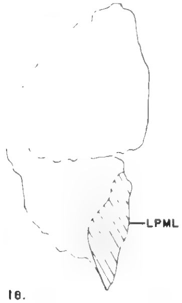

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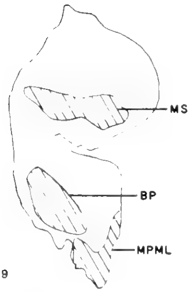

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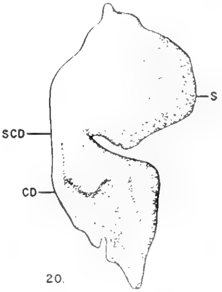

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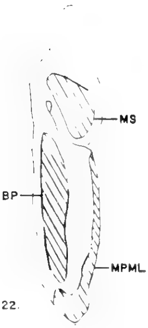

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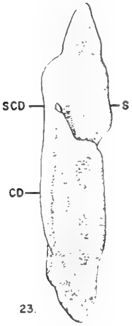

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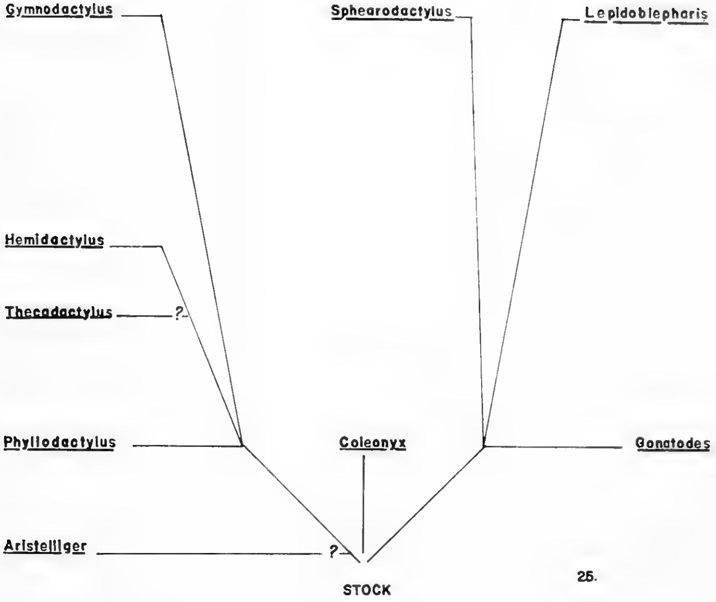
FIGURES 25-26

FIG. 25. Relationships of the gekkonoids studied as suggested by their internal otic anatomy.

FIG. 26. Representation of the percentages of the total sacculo-cochlear sensory areas occupied by each of the three sensory receptors.

FIGURES 25-26



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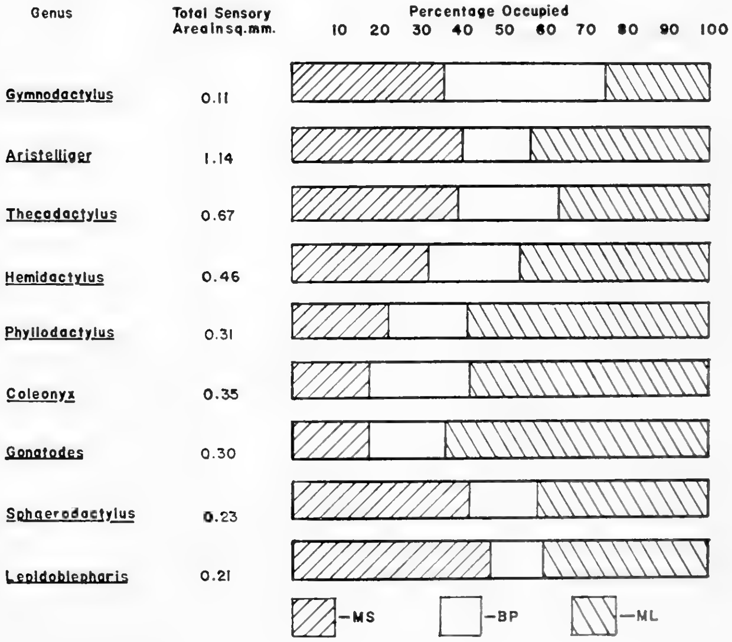

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FIGURE 27

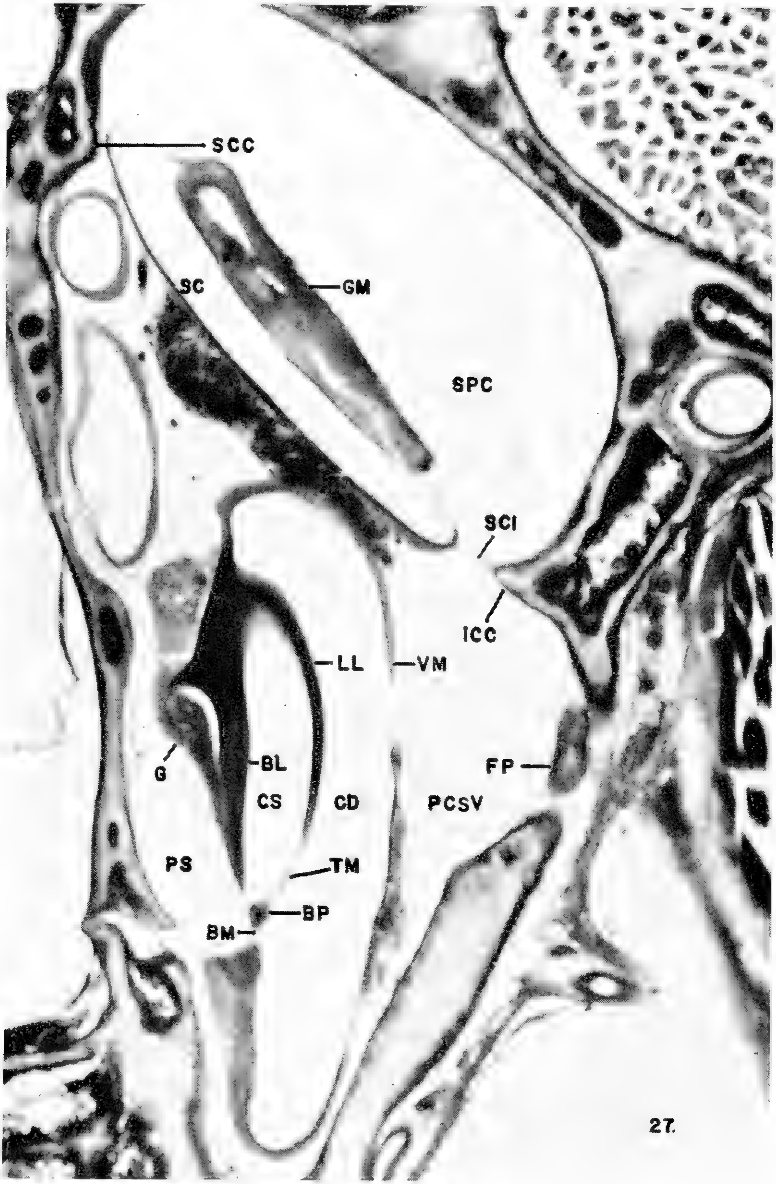

FIG. 27. Transverse section of the inner ear in *Thecadactylus* just anterior to the middle of the saccule and cochlear duct. 60×

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